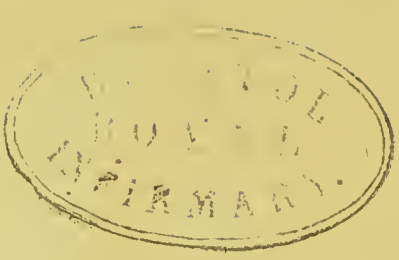
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A NEW MANUAL

OF

PHYSIOLOGY.

BRISTOL
ROYAL INFIRMARY

A COURSE OF LECTURES ON PHYSIOLOGY:

AS DELIVERED BY PROFESSOR KÜSS AT THE MEDICAL SCHOOL OF THE UNIVERSITY OF STRASBOURG.

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Translated from the Second and Revised Edition

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ILLUSTRATED BY ONE HUNDRED AND FIFTY WOODCUTS INSERTED IN THE TEXT.

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UNIVERSITY
OF BRISTOL
MEDICINE

PREFACE

TO THE AMERICAN EDITION.

During an experience as a teacher in the department of Physiology at the Medical School of Maine, I found it a difficult matter to recommend to my class an English text-book in which the functions of living tissue were closely compared and combined with its texture, or, in other words, a book wherein the relations of Physiology to Histology were carefully presented. Undoubtedly there are many good works on Physiology to which the student can refer for a knowledge of the subject; but a concise treatise within the limits of the means of most medical students cannot be found, unless we except those written either in German or French. It is not claimed that the want is completely met, but a careful study of this manual will show that human Physiology is presented in a concise and interesting manner, and that recent investigations in other countries have not been overlooked. It may be that the peculiar views of Professor Küss have been strongly set forth; but yet it must be remembered that the positive exposition of a teacher in any department of instruction is more fruitful to the cause of education than the collection of a vast amount of undigested material.

"As an indication of the general method of the author, we would direct the attention of the student to the function assigned to the *globule* or *cell* in the series of

investigations of the living organism, and particularly to the office of the epithelial globules in absorption and secretion. The time is come for science no longer to explain as phenomena of osmosis other operations of absorption, secretion, etc., which belong essentially to living bodies; but to attribute these and similar acts to those functions or offices of *globular* or *cellular* elements which are essentially endowed with life, especially as their functions cease with the destruction or death of these elements.

"With due respect for those positions assumed by our author, in this second edition we have avoided giving too great prominence to any theories advanced by him which seemed to bear too strongly towards the hypothetical, and reach too far beyond the tangible ground upon which the science of to-day rests; we especially refer to the study of the functions of chyliferous vessels as connected with the blood-vessels in the process of absorption."

The peculiarities of the original of Professor Küss and the French editor, Dr. Duval, have been conformed to as closely as consistent with the French idioms. The method of the author is concise and necessarily technical; and, although lucid, demands a systematic perusal of the work for its comprehension. An explanation of the technical terms is much aided by diagrammatic and other forms of illustration; so that the student will be rapidly advanced to a clear view of the whole, as to the subject and terminology employed.

Though an efficient compilation may be thought to serve a better purpose for the plan of a general text-book, no objection can exist against special works by expert physiologists: the special may serve as an introduction to that of wider extent.

Keeping in mind that our primary object should be to afford the most effective aid to the student, the body of materials has been enlarged and improved upon with judicious additions, new illustrations, and biographical quotations. We have endeavored to meet the want expressed in a recent review of a distinguished work on Physiology, that of "a well-digested text-book of Physiology adapted to the wants of the advanced student, which is still a desideratum in American scientific literature. If the foreign books upon any subject are more meritorious than those of our own country, the preference for them is naturally and rightly exercised. For science is cosmopolitan; and the student consults his own interests and that of science at large by supplying himself with the most useful text-books, no matter what may be their nationality." In brief, we have made every effort, within the limits assigned us by the original plan, to lay before the student (and the *physician* whose time will not allow a prolonged study of more extensive works) a satisfactory treatise on Physiology in its present stage.

LONGWOOD, January, 1875.

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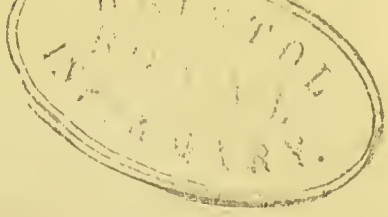
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COURSE OF LECTURES ON PHYSIOLOGY.

PART FIRST.

GENERAL PHYSIOLOGY.

I. Physiology. — Cellular Physiology.

THE word "physiology," or "physiological science," is difficult to define. According to its etymology we should interpret it as the science of growth or animation (φύειν). The word "life" or "animation" characterizes the phenomena which exist in a living being.[1] These phenomena are quite complex, and the history of seience presents a crowd of definitions, all of which are influenced by the inadequate state of the knowledge resulting from observation at different periods.

If, in the actual state of our anatomical knowledge, we examine the *organic elements* of a living being, we find that by their aspect alone we can divide these into two classes. One class is thus represented by the purely mechanical (vessels, fibres) or chemical office (different fluids) which these elements must render to the organism. Those of the second class appear to us at first inexplicable (globular forms, cells[2]), if we consider their functions either as mechanical or chemical.

If, on the contrary, we examine the *acts* of which the living being is the theatre, we meet a great number of physical and

[1] An attempt has been made to substitute for the word "physiology" that of "biology," which, by its etymology, does not signify science of life, but the different phases of life.

[2] We purposely employ the words "cell" and "globules" indifferently, though we own to our preference for the word "globule."

chemical phenomena resembling in every respect those produced by inanimate nature: thus, the eye is a physical and dioptric apparatus; the transformation of starch into sugar, in the mouth, is a purely chemical fact. But we meet, besides these, phenomena which can be explained neither by chemistry nor by physics: these phenomena deserve a separate study, and should constitute a special science in a department whose bounds are unlimited. Such phenomena are, properly speaking, vital: but at this present time we can only give a purely negative definition of life; viz., life is all that cannot be explained by chemistry or by physics.

But, whilst all the chemical and physical phenomena are localized in those portions of the apparatus that are simply mechanical or non-globular (fibres, vessels, etc.); whilst these apparatus present to us always the same essential aspect, and whilst, for example, a fibre taken all by itself can often offer no characteristic features by which we can designate it as young or old, — yet the phenomena which are neither chemical nor physical, in other words, vital phenomena, are localized in the globules or cells, so far as we can now by the process of elimination suppose; this is also confirmed by observation; these elements are presented to our view as continually undergoing changes; possessing an ephemeral existence they undergo metamorphoses of form and of composition, from the moment which we can call their time of birth to that which constitutes the time of death; in short they are endowed with age. This is precisely the essence of those phenomena which can be explained neither by chemistry nor by physics, so that we can say life is the correlation of successive phenomena presented by the globular element, and can define in a positive manner the word physiology, as the study of the globular element in its metamorphoses. Physiology in its essence can to-day be no more than cellular.

These metamorphoses are, as we have said, "changes of form and composition." Changes of composition are not necessary to characterize life, for every organic body in contact with the air will absorb oxygen and evolve carbonic acid, until it may have become burnt up or putrid. The globule, however, far from being destroyed by this change, is transformed, is multiplied. This represents its *life*. Cuvier defines this "un tourbillon" (vortex), — rather an incomplete definition, because, laying aside the changes of form, it can

be applied only to those phenomena of changes that may be likewise encountered in dead nature.[1]

These metamorphoses of globular elements are accompanied by chemical and physical phenomena that cannot be disregarded, because they figure as effects or even as assistant causes of vital acts; as, for example, the simple mechanical transportations (circulation) whereby the globules are brought together. Being obliged to study these phenomena side by side with those which we call essentially vital, we can say, in a more general sense, that the object of physiology is the study of all the phenomena that take place in the organism. Yet it is with the cell in general that we should commence our study, and around this we can then group all the rest, since the cell alone is the essentially vital element.[2]

II. Of the Globule or Cell. — Its Properties. — Historical Review.

Globules, essentially living elements, are especially characterized by their microscopic dimensions; their diameter varies between $\frac{1}{100}$ and $\frac{3}{100}$ of a millimetre; one only, the ovum, attains a size sufficiently large to be distinguished by the naked eye. This extreme minuteness explains why we could not recognize what might be called the essence of vital phenomena, until the time that microscopes gave us an opportunity of examining the extremely small objects in which these vital phenomena have their seat.

[1] *Vide* P. Ad. Rousseau, "Rôle et Importanee du Globule en Physiologie." Thèse de Strasbourg, 1866, No. 965.

[2] In the olden time, when the microseope was not known or used in the study of living tissues, various theories of vital phenomena were used to explain the principles of physiology. At one time the ageney of spirits, at another the pneuma or breath, at another archaeus, at another φλόγος, were used to explain the occult causes of these phenomena; later still a power or force called vital was brought forward. An insurmountable objection to such theories lay in the fact that these were all oecult agencies, capable of being proved simply by a process of mental reasoning, and resulting in the establishment of unsound and unavailable doctrines. The cell theory has no such objection. A cell can be seen under a microscope, and its special properties studied and classified, and the doctrines resulting are both sound and available.

Should we, after considering their minuteness, consider, first, their physical properties, and then those which are universally vital we may note: —

Their Form. — All the globules are primarily a small spherical mass, homogeneous and compact. This form they present in their early condition; but afterwards from different causes they change into a variety of forms and aspects. Thus their homogeneous substance can be divided in such a way that on the inside of the superficial surface solid particles may be grouped, whilst a more fluid substance will remain about the centre, and a kind of corpuscle will be formed, having a limiting membrane with its contents. Then the globule takes the form which merits generally the name of a cell. The cell reigns almost universally throughout the vegetable kingdom; in the animal kingdom, however, without being exclusive we prefer generally the word globule, which moreover recalls the primitive and essential form. In the condition of a cell, the vital element is composed of an amorphous envelope, and granular and transparent contents, in the middle of which a vesicle is seen, called a "germ" (nucleus), which itself also encloses another germ, called a *nucleolus*.

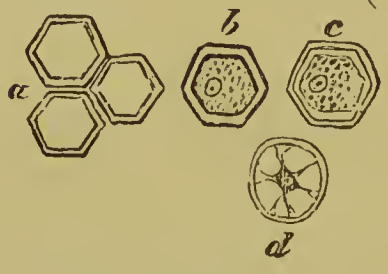


Fig. 1.
Vegetable cells (from the potato).

Among certain physiologists, all these parts (envelopes, contents, nucleus, and nucleolus) must be present in order that the term living cell should be legitimate; and even each one of these parts must have a *rôle* of its own, the contents presiding over the function, and the nucleus over the reproduction of the cell; this is perhaps a little too precise.

Thus many observers state that the nucleus disappears from the ovule at the moment the latter begins to become segmented, that is to say, multiplied; consequently the word "cell" is not so general that we could adopt it to the exclusion of the word "globule," for we do not think the perfect cell is met in every place where the phenomena of life are observed, and that these latter disappear where the cell does not exist.

Besides this grouping in the primarily homogeneous mass, the external form of the globules can undergo an infinite variety of form; as, for example, by the process of nutrition the globule becomes larger; again, compressed by its neigh-

bors, and these also pressing upon each other, most singular forms are assumed in which we ought primarily to see a sphere, which, in fact, may often be found in the deeper or younger layers. Among others, as for instance in the globules, the relations which the nerve globules must form with the nerve fibres, oblige the former to divest themselves of their typical shape to throw out prolongations in stellate form. Thus and from other causes, as will hereafter be observed, we find in the worn-out and modified globule polyhedral forms as well as laminated, cylindro-conical, fusiform, and stellate forms.

Color. — Globules generally are colorless, though certain have divers colors; the blood globule is red. Others are pigment globules, that is enclosing opaque granulations, which in men are generally dark colored.

Elasticity. — Globules generally are endowed with considerable elasticity; thus a globule flattened by some physical force so as to assume a discoid shape, may, when that force is removed, retake exactly its primary shape. This is seen when, being forced to traverse through a narrow orifice, the globule becomes elongated in a cylindrical form, and then, after emerging from the pass, again assumes its round form.

Chemical Composition. — It may be said of the globules in general, that their chemical composition is quite complicated. The dominant element is water; four-fifths of the weight of the globule is made up of this element, and this forms one of the conditions of its vitality, for water serves as the menstruum for other substances. Thus moisture may be considered as an empirical *character* of the life of a globule; cancers which are only an excess of globular life are more acute when they have a more moist consistency.

After the water in line of importance comes albumen. this substance is almost characteristic of the globule.[1] The *gluey substance*, or gelatine, which is, on the contrary, characteristic of the non-globular elements (connective and even elastic fibres), is never found in the globules.

In addition to the albumen we find always a certain proportion of fat bodies in a state of intimate combination with

[1] This is what gives to the globular masses their plasticity. Egg, liver, and kidney are very nutritious, and these masses are almost entirely composed of globules.

the preceding elements, especially in the young cells, as is proved by their transparency; *this intimate combination of water, of albumen, and of fat, is apparently one of the essential elements of the vitality of the globule;* when the latter attains its maturity, the fat bodies accumulate in it, and then only are they seen, apparently in a free state, in the form of spherical beads, giving to the cell an opaque aspect.[1] This appearance should be regarded as a sign of approaching death or at least of the old age of the globule, which will either soon undergo decomposition, or give birth to an entire generation of young elements in which the fat will be concealed. Consequently an abundance of water and of albumen, which is characterized by great transparency, is a sign of life; excess of fat, with opacity of the globule, is a sign of death. When a tumor, primarily acute, begins to present fatty elements, its tendency to disappear may be predicted.[2]

Besides these three principal elements, there are found others in small quantities, and non-essential; these are the mineral substances which make up the general composition of the body, such as potassium (in state of potash salts) and phosphorus; these two substances are especially found in the nerve elements; also sulphur, incorporated with albumen or represented by its salts. The same may be said of sodium, calcium, iron, magnesium, and even some other metals. It answers our purpose simply to note the fact that the globules are chemically very rich, which would naturally lead us to infer what part these bodies, so complex in composition, would perform in the great work of metamorphoses.

Electro-motor Power. — Without doubt it is to the multiplicity of the constituent elements that the globules owe their electro-motor power; this property of disengaging electricity is especially met with in the nerves or nerve tubes

[1] *Vide* J. Straus, "Essai sur la Physiologie de la Dégénérescence graisseuse des Muscles." Thèse de Strasbourg, 1868, No. 124.

[2] So when fat is observed in those elements where it does not belong, serious fears for the future should be apprehended. M. Küss has observed that the cancerous tint (a characteristic of cancerous cachexia) is to be looked for only when the cancer becomes fatty. Thus, by the aid of the microscope, he could tell whether a cancerous mass belonged to a person enjoying every appearance of health.

which are not globules, but derive their properties from and are in intimate association with these globules.

Tenacity of Composition. — But of all the properties belonging to their composition, the most important and essentially vital is their tenacity of maintaining their constitution in spite of the surrounding elements; and, moreover, their power or property of repelling or of assimilating certain substances by a *veritable selection.* Exposed to an atmosphere greedy of moisture, a living globule does not lose its watery constitution; it is in this way that the cells of the integument, in the animal as in the plant, maintain in the interior of the organism the moisture necessary to life. It is in this way that the blood globule, rich in potash and in phosphates, floats in a fluid (liquor sanguinis) rich only in soda and almost destitute of the preceding salts, and still the globule retains its potash, and repels the soda by a veritable phenomenon of repulsion, essentially vital. Here the laws of osmosis lose their force, for they *encounter living elements.* The same blood globule is loaded with oxygen in the lungs, and becomes the vehicle of its transport through the economy. We can also cite the example of the epithelium of the urinary bladder, which offers a perfect barrier to the passage of urine through its walls, a passage easily effected six or seven hours after the death of the patient, and then only because this epithelium has ceased in its turn to live.

In opposition to the so-called phenomena of rejection, we have another instance in which the globule favors, on the contrary, absorption: thus the epithelium of the intestine at a certain time, and under the irritation of the gastric juice, allows the absorption of the elaborated aliments, and with so much rapidity that it is almost impossible to study the details of this phenomenon.

Life of the Globule. — Its life is in our eyes the most essential characteristic of the globule. This element is born, performs its functions, and, at the end of a variable time, has a tendency to disappear by means of very various transformations. These three phenomena, birth, life, and death, constituting the metamorphoses or functions of the globule, occur only under the influence of certain excitants.[1] In the vegeta-

[1] "Matter in itself is inert, even living matter, if considered in the sense of deprivation of all free-will. Living matter, however, is irritable, and can itself enter into activity and manifest peculiar properties." (Bernard.)

We shall see that the nerve globule itself, which in the first

ble kingdom, light, heat, and doubtless electricity, constitute the most indispensable excitants. This will explain why grains of corn, found in the tombs of the pyramids, have remained dormant during long periods of years without showing any sign of life, and become awakened, or, in other words, vegetate, when exposed to external excitants. The conditions of the animal globules are none the less complicated; again, a certain form of burning produces rapid changes in the cells of human skin, in the epidermis. These exciting causes may be physical, chemical, or even may originate in the interior of the organism (being vital), and the principal of these interior (or vital) causes is most certainly that of innervation, or the influence of the nervous system upon the vital elements. Moreover, the actions of the various excitants may succeed each other, and so form a circuit of influences, alternating in character; in this way the elements of the surfaces (epithelium, epidermis), excited by external causes, excite in their turn by the mediation of sensitive nerves the nerve cells, and by means of the motor-nerves, convey the excitation to the muscles or to other elements on the surfaces, as, for instance, the glandular epithelium, and consequently we may have vital excitations produced by excitations which were at first only mechanical.

Let us note, moreover, that, with certain globules, these excitations may cause a special action: thus, the gastric juice irritates the intestinal epithelium, and no other; again, the spermatic corpuscle is the sole excitant of the ovule, and thus efficiently arouses its functional activity or its development.

Briefly, these excitants can act with varying degrees of intensity. In the highest degree these may immediately destroy the globule; thus poisons act more especially upon one or another group of globules, and thus cause their destruction.

It is difficult to explain the nature of the phenomena by which an excitant acts on a cell. Sometimes this has been compared with the so-called *catalytic action*, whose especial characteristic consists of the fact, that the body neither gives nor takes any thing from the excited body (phenomena of

place seems to enjoy free-will, can only transmit or reflect irritations that are received from different sources. Those acts which seem on superficial examination the result of nerve-spontaneity, are really only reflex actions.

contact). But it is not so with the living globule; the phenomenon is more complicated; thus oxygen excites the blood globule and modifies its form because it penetrates the globule. The epithelium of the intestine, excited by the gastric juice, undergoes a change, but if this continues too long, it becomes more opaque, etc., showing that it has received an addition of substance.

Let us now turn our attention to those phenomena presented by the globules when under the influence of physical, chemical, and vital excitants.

Birth of the Globules. — No one has really observed the formation of cells in the midst of an amorphous liquid (blastema).[1]

[1] The theory of voluntary formation of cells in a fluid more or less amorphous dates as far back as the time of Schleiden and Schwann, 1838, and even now by C. Robin. Schwann called the liquid in which the generation was supposed to take place *cytoblastema*. Raspail compared the formation of the cell in this cytoblastema to that of crystals in a liquid which held in solution the crystalline substance. Schwann had, however, observed and described the facts of segmentation, but considered these accidental and in no wise general. To-day, and especially since the works of Remak upon the formation of the blood globules (by segmentation), it is generally admitted, in accordance with the doctrine of Virchow, that every cell comes from some pre-existing cell (omnis cellula a cellulâ et in cellulâ). However, the theory of the *Blastema* or *genesis* is still defended in France by eminent histologists, by a numerous school, and especially by Charles Robin. Robin's theory of genesis, moreover, differs in many points from the ancient theory of Schwann. Thus, the media in which the genesis occurs, the blastemata (blood, lymph, interstitial fluids) are themselves the products of pre-existing cells in such fashion that the newly formed elements have come from older cells, not indeed directly, but by mediation (substitution) of a liquid. The manner of the production of the theoretical genesis consists in the spontaneous appearance of a nucleus which is surrounded by the thickened blastema; or else the mass of the blastema is divided into globular islets, each of whose centre has a newly formed nucleus. According to this the nucleolus, which may be afterwards formed, is a secondary element, whilst Schwann considers the nucleolus as the point of departure of cellular formations. In brief, formation by genesis occurs under conditions and periods that may be stated in a general way, as follows: 1st, By the formation of male or female ovula (spermatozoidal cells); 2d, by the formation of the embryonic tissues by layers of blastoderm; 3d, in the full-grown animal by the production and renewal of the epitheliums and epiderm; 4th, and finally, it is to this manner of formation that almost all

The study of the growth and reproduction of those epitheliums formed only from cells, especially the numerous pathological products, tends to prove that every globule is born of another globule (*omne vivum ex ovo*). In this point of view, the question of spontaneous generation is gradually losing confirmation by observation. Considering then that every globule springs from another globule, the type in accordance with which this generation takes place is represented by the ovum. At a certain stage, when all the surrounding circumstances are favorable, the mother-cell presents the appearance of a superficial strangulation, which gradually grows more prominent, and finally divides the primitive globule into two globules. As soon as the first division has been accomplished, another strangulation occurs at right angles to the first; — thus finally subdividing each globule, so that, in the place of our original globule, we have four globules. We shall have occasion for the detailed study of these phenomena, when we consider the formation of the different globules, in particular the ovule, under the head of segmentation of the vitellus. Suffice it now to mention that in a general way every cell is born of another cell by the process called segmentation, and when this segmentation concerns only the portion contained within the envelope, it is called *Endogenesis*, or when both envelope and contents are involved, forming thus



Fig. 2. — Various successive degrees of intersection and segmentation of a globule (ovum from frog, *Baer*).

the pathological neoplasms owe their origin. In all other cases the cellular theory asserts its rights.

In a recent work, Onimus published a number of experiments which seem to prove that the globular elements (white globules of blood and of lymph) can be formed in the serous fluids, in lymph maintained under proper conditions of temperature, of surrounding media, and of molecular changes. This work has met with considerable opposition, and it is not right to pronounce now upon this point. We may draw our conclusions in the following words of Frey: "Though every thing seems to prove that the animal

a homogeneous mass (which is correctly speaking a globule); this constitutes fissiparous propagation (one variety only of which is the budding). The latter method is the most frequent means of proliferation; thus all globules resemble each other, not only with respect to their mode of origin, but even as to their primitive globular form.

Function of the Globules. — When once formed, globules under the influence of certain excitants perform their functions in different ways. One kind are simply endowed with the property of changing their shape; as, for instance, certain globules of the skin of the batrachians, under the influence only of light as an excitant, change from a spherical into a stellate and even a fibrous form.[1] This change of form is what was for a long time recognized under the name of contraction. So the blood globules, when exposed to oxygen, become more flat than before, a phenomenon which can also be effected by the presence of sodium chloride, and certain other neutral salts; and this would seem to prove that the change is due to a chemical phenomenon. We could also cite as examples of change of form or of contraction the movements of the vibratile cilia, with which the free surface of certain of the epithelial cells are provided, which movements certainly are connected with cell life and in no wise dependent upon the medium of the nervous system, since forty-eight hours after death they can be made to reappear under the influence of a dilute solution of potassa or soda.

Finally, all that has been said of the cells under the head of composition, tenacity of self-maintenance, the attraction they exercise on certain chemical substances, their electromotor power, etc., constitute their life. Farther on these elements of vitality will be considered separately for each globule. It should, however, be here remarked that, wherever in the organism vital manifestations are observed, these are found localized in special cells; for instance, certain cells in the liver secrete bile, others sugar, or a glycogenic substance; again sensibility is localized in the nerve cell, etc.

cells cannot be formed spontaneously, it is not without interest, nor, perhaps, without advantage, to find defenders for the ancient theories and enemies to the new (cellular) doctrine. Science will be thus placed in a position to furnish to the facts every support which belongs to them, and the study of the tissues can but gain thereby."

[1] These changes of form involve changes of color, even in globules containing no pigment.

Death of the Globules. — The globule being essentially ephemeral, at a certain stage after the special manifestations of some of the above-named phenomena, it becomes transformed and disappears. However, some of them may continue in the cell condition for many years, but they no longer live; they pass into a dormant state, which can even be compared with their death. This fact is very common in vegetable life; it is rather uncommon to see in man cells whose functions have ceased, or which have lost their characteristic vitality, though still preserving their cellular formation. We can cite, however, certain pigment-cells, those of the uvea (pigment at the posterior surface of the choroid and iris) which no longer manifest the physical properties of their pigment, but by the absorption of the luminous rays of light preserve thereby the functions of the eye intact. We could also cite in this connection those globules to be hereafter studied under the name of embryonic or plasmatic cells. These seem to lie dormant in the midst of connective tissue; but when submitted to an exciting influence suddenly awake, and spring into action, either in the restoration of breaches made in the tissue, or in giving origin to new products, generally of a pathological character. But the real death of the globules, the final loss of their individuality, may happen in two ways.

In the first case, the globule has little or no specified form. It may, indeed, dry up and fall into a state of fine dust (furfuraceous deposits, and continued desquamation of the surface of the epiderm); these scales, and pulverulent remains that constitute the epidermal scales, can be made to resume their cellular shape by being placed in an alkaline solution; still this is simply the corpse of the globule, a simple physical imbibition, and the regenerated globular form is only a form; there is no longer life. Yet, most frequently, the globule becomes infiltrated with fat, or other matters upon which it may exert a powerful attraction; in this case it becomes liquid, and falls in the form of deliquium, and thus may result various kinds of fluids. This is the mechanism of most of the secretions, and so also of most of the fluids secreted.

In the second case, the globules lose their globular shape, but give birth to many new anatomical forms, in soldering or fusing one kind with another; as, for instance, to form fibres, or canals. This is the origin of the non-cellular portions of the organism; fibres formed in this way can no longer exhibit the vital properties of those globules from which they were

begotten, but only possess characteristics distinctly physical, such as elasticity, toughness, etc. However, there are some, forming a separate class, which possess even in a higher degree the properties characterized by the primitive globule, as, for instance, the muscular fibre, which, in addition to its elasticity, is endowed with an electro-motor as well as even a still more essential property, that of changing its form under the influence of excitants. The nerve fibre possesses properties not exactly similar to the above, but yet highly characteristic of the condition of life.

These are the principal phenomena presented by the general review of cellular physiology. As before remarked, they all occur under the influence of excitants or irritants. We have shown how these may be divided into physical, chemical, or vital, this division being sufficiently accurate for the physiologist, though the most diverse excitants may cause the same effect; for example, a shock or simple touch brings about cellular contraction, especially in the muscles; electricity, or certain acids even, produce the same phenomenon, which is naturally, in the physiological condition, almost exclusively manifested under the influence of the nervous system. A more interesting division would be based upon the nature, not the effects of the excitant. This, unfortunately, is impossible. Yet, following out this plan, some have tried to recognize three kinds of irritability: irritability of formation or of development, trophic or nutrient irritability, and functional irritability. We have, however, seen how the different phenomena of development, nutrition, function, and even death, form a physiological product that should artificially be subdivided for convenience of study.

Can the irritability of development be separated from that of nutrition. Have we not also seen that cells, those of the glands, for instance, perform their chief function by disappearing as a cell element, and then becoming liquefied, appear as a secretion? An attempt has been made to divide the functions of the isolated globule as well as those of the entire organism into three great classes, viz.: relation, reproduction, and nutrition, as if the functions of reproduction were not concerned in either of the two other divisions.

The theory that life resides in the excitable elements reacting differently with different excitations, is quite ancient, and the history of the words *excitant*, *excitability*, and of those synonymes which have turn by turn taken their place, as, for instance, *irritant*, *irritability*, *incitant*, *incitability*,

etc., make up the true condition of physiology, as well as of the science of life, or science of living matter. An era of complete darkness, that is, of pure hypotheses, followed the time of Galen, who had with difficulty enounced this theory.[1] Neither Descartes, Newton, nor Boerhaave had any thing to do with physiology; they simply applied the facts of mechanism and physics to living beings.

Glisson (in 1672) was the first to suggest the word "irritability," which he considered a characteristic property of living beings; a property determining the organic movements, and which is set in motion by causes either from without or from within, which he calls irritant causes. But these theories by which Glisson characterized life in a manner so remarkable for his time, passed unnoticed by his contemporaries; and we see with Stahl (1708), and then with Barthez, the teaching of the *animists* and the *vitalists* coincide almost exactly with the ancient theories of a fundamental force (ψυχή), upon which depend all the manifestations of life.[2]

[1] The aneients, among them Hippoerates, Plato, and Aristotle, being almost entirely without observations or experiments, were busied with the *essence of life*, founded on pure hypothesis, characterized generally by their belief in a principle of life distinct from matter (ψυχή of Aristotle), hypotheses which were soon to reappear under the name of animism and vitalism. Galen, turning his attention to anatomy, rejected the purely speculative doctrines, but still his physiology was only a logical inference from anatomy, for, wisely keeping within certain bounds furnished by his observation, he sought only the part played by the different organs (*de usu partium*). This should be the true spirit to preside over the study of physiology. Under such an idea Galen deserves indeed the title of "The Father of Physiology." The physiologists of the present time add only what has been obtained by means of investigation, and consequently obtain results far different. Being able to study the organs only maero-graphically, Galen was obliged to look upon their functions simply as nearly mechanieal; now the microseope reveals to us the globule, which, in the order of things, we ean eonsider as the strictly vital elemcnt. Studying the properties and functions of these cells in the same way that Galen studied those of the organs, we may perhaps attain the true knowledge of vital phenomena, without having rceourse to hypotheses: life will be really represented by the cell reacting under the influenee of exeitants. An organ, even the whole organism, will be a union of cells, as an association is a union of individuals. (*Vide* Cl. Bernard, "Leçons sur les Propriétés des Tissus Vivants." 1866.)

[2] Stahl would not admit that living matter had vital activity or

With Haller reappears Glisson's expression, "irritability." Though but theoretically showing that irritability was a property of living matter, Haller experimented directly upon living animals; his vivisections gave him an opportunity especially of studying muscles, and he applied the word "irritability" particularly to the muscular system; if he went no farther, still he used the experimental method of study, and the theory of irritability took its definite position in science. Brown (1780) generalized this term under the special names of "incitability' and of "incitants" (*incitamenta*), giving a name to that property possessed by living matter, of performing its functions under the influence of external causes, without the intervention of any distinct principle of the organism.[1] Tiedemann carried out the same principle by substituting for the words "incitants," "incitability," those of "excitability," and "excitants." But yet, if the words "excitability," "incitability," or "irritability," in spite of their variety, express a real property, the value and limitation of the words "living matter," to which these authors attribute the property, is not precisely defined. Moreover, they do not agree in regard to its definition. Haller seems to consider that the muscle almost alone is irritable, whilst Brown considers all the solid portions of the organism are incitable; but not so with the liquids. And again, Tiedemann would allow excitability to both liquids and solids. This confusion existed even to the time when general anatomy was founded upon histology, as revealed by the microscope. Now the cell must be recognized as the primitive element of the organism. We have seen that it alone is the seat of vital phenomena, that it alone is excitable in some tissues; as, for instance, the muscles, which, being de-

irritability, and supposed a vital force, independent of organic elements, an immaterial substance, the soul (not to be confounded, however, with the soul of philosophers and theologians, which is not the same as that which is called "soul" by physiologists), which is endowed with absolute free-will, and presides alone over the functional movements of our organs. Such is the animism of Stahl, which later reappears in several schools under the name of vitalism. The vitalists substitute simply for the word "soul" "vital force," or "vital principle," a hidden quality, a fundamental force whence spring all the manifestations of life.

[1] The whole medicine of Broussais is but a theory of incitants imported from physiology, and applied to pathology. These are pathological incitants, and all diseases come from irritations. For details *vide* Cl. Bernard, "Propriété des Tissus Vivants."

rived from cells, have preserved these properties. The irritability of Glisson and Haller, the incitability of Brown, the excitability of Tiedemann, are precisely the characteristic property of the cell, and in this point of view the exact expression that the essence of vital phenomena represents to us.

It is due then to the powerful means of study furnished by the microscope that we owe the idea that we are formed from vital phenomena; but it would be unjust not to mention in this connection the name of Bichat, who, by his endeavors in the study of *general anatomy*, pointed out the fact that the foundation of the science of histology should be established by means of *micro-graphy*. The introduction of the microscope in the seventeenth century in the hands of Malpighi and Leeuwenhoek resulted more in observations of simple curiosity than in scientific researches, at least for the study of animal tissues. At the commencement of this century, Bichat founded general anatomy, and aimed at the study and classification of the human tissues; but making use only of dissections by the unaided eye, of chemical reactions, and of physiological and pathological investigations, he could grasp but a few of the gross characteristics that distinguish the tissues. But as soon as the path had been pointed out, and the microscope was established for the research of organic elements, Schwann was enabled in 1839 to attempt the study of the tissues, by starting with the cell and founding histology, or what might be called *general anatomy studied by means of the microscope.* Physiology and Pathology were the necessary consequence.

III. — Different Kinds of Cells. — Their Particular Functions. — Diagram of the Organism. — Plan of Study of Physiology in this Treatise.

At its origin an organism is formed of a single cell, the ovum, which has already been mentioned, and whose *segmentation* has also rapidly been described, as a type of generation or of proliferation of the class of globules in general. From the segmentation of the *vitellus*, or contents (protoplasm) of the ovum, the envelopirg membrane, or *zona pellucida*, is formed, enclosing a large number of globules resembling each other; but after a while these globules begin to vary in their form and position.

At first, these globules are grouped towards the periphery of the cavity of the primitive (Fig. 3) ovum, and, in this way, form a membrane which we shall study under the name of epithelium. As in the perfected organism, an epithelium rests upon a fibrous or undetermined tissue, so also does the *ovular epithelium* rest upon the *membrana pellucida* (Fig. 3, A). We see then even at this stage (and great importance must be attached to these forms) the organism represented successively by a cell, and secondly by an epithelium; this latter might be called *epithelium of the zona pellucida* (Fig. 3 B); and as this serves as the germ of all the other portions it has been called the *germ-membrane*, or, more generally, blastodermic membrane, or blastoderm.

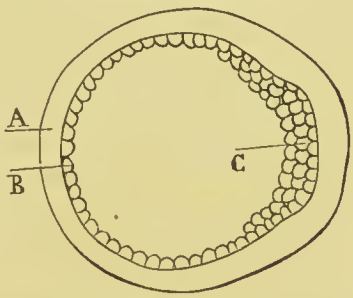


Fig. 3.
Diagram of the Blastoderm.*

This change of position of the globules, whence a globular membrane results, is soon followed by a change of form, whence there occurs a separation into distinct layers in this membrane; take for example one of the meridians of the blastoderm where the globules become multiplied more than in any other place; here the blastoderm, as with every epithelium which becomes hypertrophied in a certain portion, is obliged, as will be seen later in the formation of glands and papillæ, to swell out and form a sort of pouch on which may be lodged the new globules that are formed. This pouch or villosity (Fig. 3 C) is the first rudiment of the embryonic body. Without now going into the details, it is necessary simply to mention that at this point the globules become separated into three layers or folds, viz., the external, internal, and intermediate folds.

The *external fold*, called the *corneal*, maintains its globular condition, and from this is formed our *epiderm*, our external cuticle,[1] and such of the organs as may be derived

[1] A comparison of the two kingdoms demonstrates the fact that both animals and vegetables have an external envelope, composed of analogous cells; so that we can apply to each the name cuticle. Yet in the vegetable the cuticle is very simple, and almost everywhere the same, but in the animal it is complex, and, accord-

* A, Vitelline membrane. B, Simple form of Blastoderm. C, Point where the Blastoderm is already composed of three layers of cells, three folds.

therefrom (we shall see farther on whether the nerve globules are derived from the external or the intermediate fold of the blastoderm).

The internal fold will give, by means of the envelopment which forms the internal cavity of the embryo, the *internal cuticle*, or the epithelium of the *future intestinal canal* of the embryo, and also the numerous adjuncts of this canal, most of the glands, and also the lungs.

The globules of the intermediate folds undergo transformations which are much more complicated; some are transformed, by the mechanism already mentioned when treating of the globules in general, into muscular, nervous (perhaps also into nerve cells) elastic, and connective fibres, and other forms of the connective tissue; others remain in the condition of globules, though changing their form; and again others become fused with the fibrous elements of the connective tissue (embryonic globules, cells of cartilage, of bone and of tendons) and others bathe in a liquid (blood globules); thus, in short, the intermediate gives origin to two globular forms, viz., the embryonic cell and the blood globule (and possibly the nerve-cell.) [1]

The elements of the external cuticle, and those of the internal cuticle or internal epithelium being then united in the single term epithelial (or lining) globules, since they line the surfaces[2], we have but four kinds of globules to study, viz., the epithelial, the nerve, the blood, and the embryonic globule.

1. Epithelial globules, placed upon fibrous membranes, destined only for their support, form the sole living portions

ing to whether it covers all the superficial parts of the body or the cavities communicating with the exterior, it is either internal or external.

[1] This distinction of the blastodermic cells may at first seem surprising, though a similar phenomenon is continually passing under the observation of every surgeon. In a fresh superficial wound, there appears first a mass of globules, primarily alike, which separate themselves so as to become either epiderm-cells, connective fibre, etc., before the cicatrix is formed, and exactly in the same way as in the folds of the epiderm.

[2] In fact, the word "epithelium" was primarily used to designate the epiderm of the nipple, and afterwards to designate the epiderm of the mucous membrane, to which there is now a tendency to limit its application.

Astruc says: "La peau fine et délicate qui recouvre le mamelon, et qu'on appelle Epithelion" (επί, θηλή; upon, the nipple).

of these membranes, and, according to their functional activity, they present differing forms; if they are situated in a region where their functions are not very active they are few in number and in order to occupy completely the surface given up to them, they are flattened out, forming a sort of pavement, and hence are called *pavement* (or tessellated) *epithelium* (Fig. 4, A). If, on the contrary, as, for example, on the more important mucous membranes, their vital functions are very active, they become multiplied, accumulate in large numbers upon the same place, and make room for each other, by being compressed sideways; and so instead of being round they become cylindrical, hence they are called *cylinder* (or columnar) epithelium (Fig. 4, B). Finally, if a simple layer is insufficient, the globules are superposed, and hence are called stratified epithelium (Fig. 4, C).

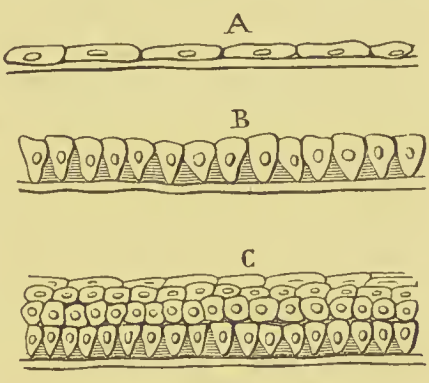


Fig. 4.
Various forms of Epithelium.*

Moreover, for the purpose of offering a large surface without occupying too much space, these epithelium cells overlap each other, an instance of which may have been remarked in the blastoderm, and according to whether the overlapping is on the superficial surface or on the side near the deeper tissues, these make up papillæ or glands; more particular mention will be made of this subject when we have occasion to speak of the formation of the epithelium of the mucous membrane of the mouth.

The functions are of far greater importance than the form of the epitheliums; these may be divided into three classes. Certain of the globules present an obstructing surface to the passage of fluids, &c., and are impermeable, as, for instance, in the epithelium of the bladder and of the serous membranes in general. These might be called *neutral* globules.

Another class, on the contrary, absorb very actively the substances (gas or liquid) brought in contact with them, and transport these to the more distant and deeper portions of tissues, as is done for instance by the blood globule. These may be called *absorption* globules.

* A, Pavement epithelium. B, Columnar epithelium. C, Stratified epithelium.

A third class possess a faculty of drawing to them certain substances contained in the neighboring tissues or fluids, and thus free the organism from which these are detached. In this way the scaly portions of the epiderm, before passing into this condition and falling off, attract certain calcareous salts, and more especially the phosphates which are contained in the organism. This is also an example of the functions of secretion, and these are called *secretion* globules. These globules, more than any of the others, are characterized by ephemeral existence, and form the largest portion of glands; the mammary gland is nothing but a membrane of canaliculæ, covered with globules which possess at certain times an excessively active life; then they become very rapidly transformed, and their remains constitute the milk.

2. The nerve globules (or cells) are not fixed upon surfaces under the form of membranes, they are hidden in the deeper parts, constituting what has been called the gray nerve-tissue. By direct experiment it is impossible to judge of their life. Yet, like the others, these globules seem to live, and are nourished, and though we cannot judge *de visu* of their transformations, at least by comparison upon the dead body, these are found differing in appearance and age, some being smaller and transparent, others greater, pale, or filled with granulations, thus indicating a commencement of their decay. Influenced by their metamorphoses, these globules, as well as the nerves with which they enter into communication, are electro-motor. Indeed it is these prolongations or nerve tubes by which the nerve globules are characterized, and which give them their stellate form.

3. The *blood globules*, whose existence is best known and the most accessible to our senses, form in blood, and consequently in the body about one-twelfth of our whole weight. They differ from the preceding globules in the fact, that instead of having a fixed place they course through the whole organism; their discoid shapes render their transit easier, and during their course they are continually being transformed, certain of them perishing in order to give room to others. During this nomadic state, the blood globule is still characterized by the phenomena of repulsion and attraction, changes of form and composition, loading itself at certain places with chemical products, which seem destined for deposition in other places.

4. The embryonic cells are so called, because they are the same in the adult that they were in the embryonic stage;

distributed in the midst of the tissues, they continue to serve for the production (the periosteal cell continually forming bone) or for the reparation of breaches which may have accidentally made a rent in or destroyed the tissues; hence also their name plasmatic cells. Some of these, *incertæ sedis*, help sometimes by means of the circulation to nourish the tissues where they are distributed, and then are seen in star-shaped form with anastomoses of their prolongations; the cornea offers a beautiful illustration of this distribution (Fig. 5).

At other times the plasmatic cells undergo a sort of decay, by accumulating fat in their interior, and thus afford adipose tissue; in this condition they are no longer susceptible of undergoing transformations; they are so to speak dead. But most, though changing form and becoming almost mummified (stellate plasmatic cells), preserve, in their latent con-



Fig. 5.*

dition, all their vital characteristics, ready to wake up if the excitation is sufficiently strong; in this way they can furnish new forms, as, for instance, cancer, different tumors, and, in general, purulent abscess globules. In this way the embryonic cells become pathological.

Supposing now that we are familiar with the different kinds of globules, excepting the embryonic globule, we can represent them in a diagram, grouping together the functions of the three classes of globules.

We can represent the organism as a homogeneous mass, more liquid than solid, on the surface of which is a layer of

* Section of cornea cut parallel to the surface. Stellate corpuscles, with their anastomotic prolongations (*His*).

cortical or epithelial globules (A A A), of which some absorb, others excrete, and finally others are impermeable or neutral. In the interior, towards the middle far from the surface (Fig. 6, B), are found a group of globules, relatively permanent; viz., the nerve globules, which by means of their prolongations are in communication with the peripheral globules so as to be excited by one set and to react upon another (reflex actions). Thus the blood globules travel from the periphery towards the centre, and *vice versâ* (Fig. 6, C C); and this circular current draws towards the centre the elements of nutrition absorbed by certain globules from the surface, and draws the decayed portions of the globules at the centre towards the globules upon the surface, which are then thrown off (excremental secretions). The blood globule thus acts as a medium of exchange, the same process in lower animals being effected by imbibition.

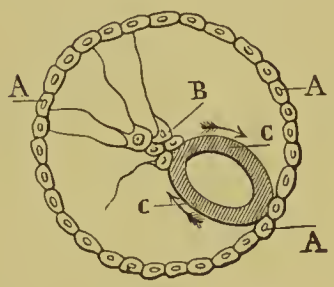


Fig. 6.
Diagram of the organism.*

Though these are the more simple forms of globular activity, yet it must not be forgotten, that these phenomena are also linked with those belonging to chemistry and physics, which likewise should be studied at the same time; as for instance the blood globule seems to be of service to the nerve globule by establishing for purposes of nutrition a communication between this deep-seated globule and those at the surface; but its circulation requires the intervention of the nerve globule, which may excite the muscular fibre, and thus give rise to certain mechanical phenomena of hydrostatics, etc.

Now it may be noticed that the collection of the phenomena of animal life constitutes a living chain that must be artificially broken for convenience of study. The most striking phenomena is the wandering of the blood globule; it might most naturally seem that the commencement of our study should be with this phenomenon; but we prefer to commence first with the nerve globule, which will lead us to study, secondly, the non-globular forms (muscles) with which it is connected; and subsequently the movements and other mechanical and

* A A A, Globules from the surface, epithelium. B, Central nerve-globules, with prolongations coming from or going to the surface. C C, The circle of circulation of the blood.

physical phenomena of the organism, as well as the tissues which are its seat. Then we shall consider the blood globule and its circulation, and finally, prepared by our knowledge of the accessories, we can more readily comprehend the more intricate relations of the internal and external coverings, and especially the epithelium of the genital organs, as well also as our point of departure, the ovum.

PART SECOND.

NERVOUS SYSTEM.

I. Nervous System in General.

1. *Anatomical Elements.* — The nerve globule partakes of the general properties of the living globule; its dimensions are very small (one to eight-hundredths of a millimetre); but it attains in certain regions larger proportions, and may even with a little care be seen with the naked eye. The nerve globules are looked upon as cells having an envelope (?) enclosing protoplasmic elements, a nucleus, and a nucleolus.



Fig. 7.—Nerve globules, their prolongations, nuclei, and nucleoli.*

These globules are generally stellate, that is to say, provided with prolongations (Fig. 7); at this present time globules having one prolongation are called *unipolar*, those having two prolongations, striking out in the same direction or

* *a*,*a*, From the deep portion of the gray substance of the convolutions of the cerebellum. *d*, Cells from the posterior portion of the gray substance of spinal cord (dorsal). In all these globules the prolongations are more or less torn.

oftener in opposite directions, are *bipolar;* but most of them are *multipolar*, and may have as many as ten prolongations. These prolongations are ordinarily quite long, and constitute the *nerve fibres.* (Fig. 8.) These fibres are composed of a thin envelope (*vv*) (forming Schwann's sheath) encircling a medullary substance (myeline, *mm*) which may easily be decomposed into little drops of fat, and in the centre of this a thin axis cord (*a*) discerned with difficulty, the axis cylinder. Some fibres may be reduced to simple axis cylinder and to the peculiar sheath of Schwann without any medullary substance (fine fibres or filaments). The membrane of Schwann and the medullary sheath serve only for the protection and isolation of the axis cylinder.[1] The axis cylinder thus appears to be the most important part of the nerve tube. Finally there are found in certain nerves, and especially in the branches of the great sympathetic, flat, pale, or amorphous fibres, rarely fibrillary, and furnished with very distinct nuclei (Fig. 8, A) : (gray or gelatinous fasciculus) ; these are the fibres of Remak, which some physiologists (Morel) consider as belonging to the connective tissue, though the nerve character of these fibres is indicated by the history of the development of the nerve fibre, and by the study of the pale nerve elements in the lower animals.

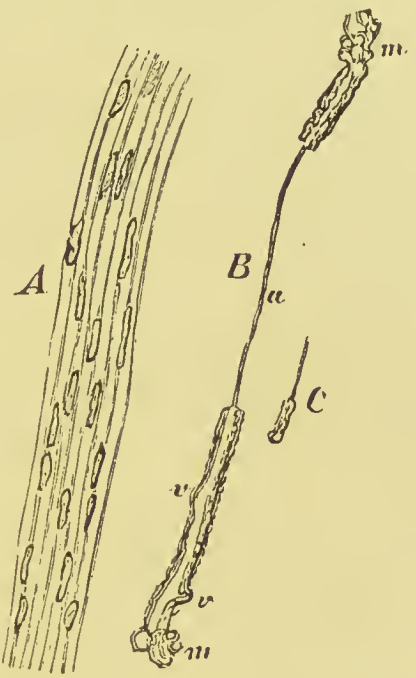


Fig. 8. — Gray and white nerve fibres.*

[1] Recent histological researches by Ranvier appear to show that the nerve tubes are formed of *cells joined together at the ends.* He has also ascertained that the substance of Schwann does not form a continuous cylindrical axis, as has been hitherto supposed, but exhibits at regular intervals constrictions in the shape of rings.

* A, Gray fasciculus, gelatinous, from the mesentery, treated by acetic acid. B, White primitive fibre, from crural nerve. *a*, Axis cylinder exposed. *v,v*, Fibre, with its medullary sheath, becoming varicose and oozing out in drops at *m,m*. C, Primitive fibre from brain, containing no myeline. 300 diam. (Virchow, "Cellular Pathology.")

It might be added that in certain little trunks, isolated from the great sympathetic nerve system, the number of these pale fibres is so large, and the number of tubes with medullary substance so small, we are obliged (especially in the splenic nerves) to consider Remak's fibres as true nerve fibres.

If these prolongations of the nerve globules are followed up carefully, the nerve tubes will be observed, after a shorter or longer distance, to be connected, in fact joined, with a neighboring or a distant globule, or sometimes with several of these. Thus in the spinal cord there are globules whose ramifications connect them with other globules. Sometimes the nerve fibres, on the other hand, terminate in muscles (motorial end-plates), or even in organs which are at present but problematical (tactile bodies), and which are specially found in the skin. It may also be noticed that generally nerve fibres are only commissures or bridges projecting from

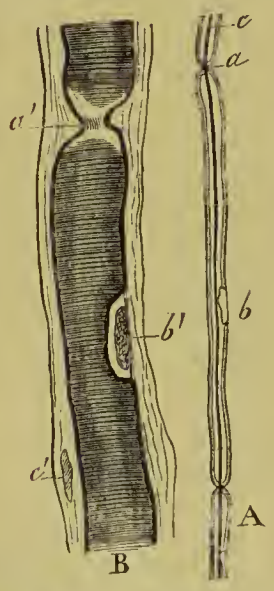


Fig. 9.—Nerve tubes, according to Ranvier's researches.*

These constrictions, plaeed at distances varying according to the dimensions of the tubes, enclose segments whieh are ealled *interannular segments*. Each of these appears to represent a cell; indeed, in the eentre of each, and on the inner surfaee of the substanee of Sehwann is found a flat oval *nucleus* (Fig. 9) floating in *a sea of protoplasm*, with whieh the tissue is lined. Farther in is found the *myeline*, whieh, eonsidered in regard to general morphology, bears the same relation to the interannular segment as the fat in an adipose cell does to the eell. The signification of the eylindrieal axis, which runs uninterruptedly through the whole series of segments, has not yet been definitely aseertained from the standpoint of general morphology. The study of the degeneration of the nerves after section, seems to confirm the foregoing eonelusions as to the nature of the interannular segments, without, however, yielding us any more preeise information as to the nature of the axis eylinder, whieh is, notwithstanding, the essential element of the nerve tube. Indeed, it seems probable that the other appearances are simply due to the artificial methods used in the preparations.

* A, Nerve tube under low magnifying power. *a*, Constriction. *b*, Nucleus of interannular segment. *c*, Axis cylinder. B, The constriction and part of interannular segment, seen under a higher power (prepared with osmic acid). *a'*, Constriction. *b'*, Nucleus in segment. *c'*, External nucleus in sheath.

a nerve globule to an element of another variety, or simply to another nerve globule.

These nerve fibres seem to be only a physiological supplement to the globule from which they originate; every excitation of the fibre is retained by the globule, and *vice versâ:* the fibre disconnected from its globule undergoes a degeneration (fatty) more or less complete.

2. *Life of the Nervous System.* — This physiological whole (globule and its prolongations) lives and is nourished: the nerve centres, composed practically of globules, need an enormous quantity of material, and give back to the surrounding media (by means of the blood) a large quantity of refuse matter. The mass of nerve fibres (nerves) consumes likewise some materials, and produces refuse matter; they in other words are fed; they are very vascular, and when the supply of blood is shut off, phenomena resembling decomposition may be observed.

It will be noticed, farther on, that the materials consumed by the muscles during their activity are principally hydro-carbons (sugars and fats) and also albuminoids in small quantity. On the other hand, the nerve element seems to require albuminoid substances; and the more intense the nerve work, the greater will be the amount of refuse material, caused by combustion of the albuminoids (especially urea), in the excretions, in the urine, and in the products of the liver. According to Biasson (1868) the amount of urea excreted by man varies according to the amount of cerebral activity. Again, Oscar Liebreich has shown that, in animals who have been made to die by pain, after cutting the sensitive roots of one side of the spinal cord, this side (reduced to inertia) would consume less protagon than the other side. Protagon, whose composition is not yet defined, seems to be a compound of fatty phosphates and *neurine*, and serves for the nutrition of the nervous system, to which it is carried by the blood globule. According to Austin Flint, Jr., the excrementitial product formed by the disassimilation of the brain and of the nerves, at the expense of protagon, is represented by cholesterine, which is separated from the blood by means of the liver, and then thrown into the intestines. This view is based upon a number of experiments, which show, moreover, that the excretion of cholesterine is in direct ratio to the nervous activity. The common expression, "to feel bilious," seems justified by one of the elements of the bile, viz., cholesterine.

These acts of nutrition produce in the nerves a disengagement of forces, which are brought to light by electrical currents; this phenomenon, though not directly observed in the nerve globules, is very evident in the peripheral nerves.

In the state of rest certain currents are constantly traversing nerves, going from the surface to the interior, and acting as if the nerve fibres were the seat of two enclosed elements, the extremity being positive and the centre negative. In fact, whenever by means of a galvanometer, a communication is made between the external surface and the surface of the section of a nerve, a current is observed to pass from the periphery towards the centre. This electrical phenomenon, called the *electro-motory force of the nerve*, disappears or becomes feeble whenever the fibre is subjected to an irritation, or whenever it acts as a conductor, or in fact whenever it performs its proper function; a disappearance of the *electro-motor power* is called *negative oscillation.* It has been surmised that at this moment nutrition is arrested, and with this ensues the normal current of a state of rest. The deduction can easily be drawn in what way the fatigue of the nerve may be brought about, and why an irritation too long maintained may cause destruction, which latter may also be accompanied with pain.

But, on the other hand, direct experiment shows that the nerve in functional activity does more, — there is produced a development of heat, the existence of which Schiff has just demonstrated in the nerve-centres, influenced by fear, or excitement of the senses, or from every cause which may produce cerebral activity. It may be that the negative oscillation indicates that electricity of the nerve in a state of repose is transformed into heat in the active state. (In regard to this see farther on an analogue of the negative oscillation, in the study of the muscles, and also the transformation of one force into another force.)

3. *Action of the Nervous System.* — What constitutes the special function of the nerve apparatus, both fibre and cell? — This consists essentially in a phenomenon called reflex. When a nerve fibre is irritated, this irritation is transmitted to globules more or less distant, and from the latter to the peripheral parts. Most generally this irritation is upon a tactile corpuscle or

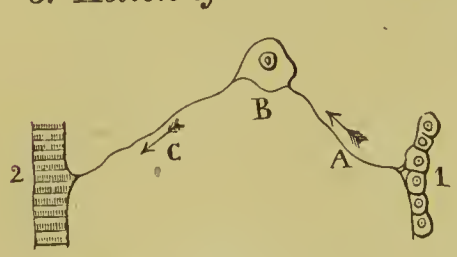


Fig. 10.
Diagram of a simple reflex action.*

* 1, Surface (epithelium). 2, Muscle. A, Centripetal fibre. B, Central nerve cell. C, Centrifugal fibre. A, B, C, form the *nerve arc*, which presides over the reflex action: the diastaltic arc of Marshall Hall. A represents the *eisodic fibre*; B, the central excito-motor; and C, the *exodic fibre.*

some analogous organ (adjuncts of the peripheral surfaces); it is transmitted by a *centripetal* fibre to a central globule, which reflects this by a *centrifugal* fibre to another organ more or less peripheral, as, for instance, a muscle whose contraction may be thus effected, or to a gland which then pours out its secretion.

Thus fibres perform their function of carrying the excitation towards a globule, or of transmitting it from the globule to the periphery; hence the names centripetal or sensitive given to the former nerves, and centrifugal or motory to the latter. This name should indicate merely that this is the sense in which the function of the fibre is manifested to us, but no essential difference between centripetal and centrifugal filaments are intended, as we shall soon see that direct experiments demonstrate the contrary.

The office of the globule is to favor the transmission of the excitation from one to another fibre; oftentimes, indeed, the first globule reflects its action, by commissural fibres, upon one or several other globules which can turn the action in a different direction again, either directly upon a centrifugal fibre, properly so called, or upon some fresh nerve globules: the globular elements can even absorb or enfeeble the action, or even store it up, as it were, in a latent state, and send it off only at another time, when influenced by new excitations. Hence we see that reflex centres present very complicated phenomena, becoming at one time centres of diffusion, and again of co-ordination of movements, of memory, etc.; these centres can be also the seat of sensation for the peripheral excitations.

Leaving out of mind the central phenomena that are difficult of analysis, we see that the office of the nerves is essentially that of conduction. Now what constitutes conduction, and what is the peculiar phenomenon by which it is characterized? For a long time this was supposed to resemble and partake of the nature of the electric current; but at the present time it is proved that the *nerve influx* has nothing to do with electricity. In the first place its rapidity of propagation has been calculated to be 28 to 30 metres to the second, a very different rate from that of the electric current, and even this varies with the temperature of the nerve; according to Helmholtz, in frog's nerve cooled to a temperature of the freezing point of water (0° c.), the rapidity of the nerve agent is but one-tenth of what it is at 15° or 20° higher. Again, when the nerve performs its functions, in-

stead of producing electricity, there is, on the contrary, negative oscillation (as has been before remarked), that is a weakness or disappearance of the normal current of repose.

In a nerve displaying activity, there appears to be a sort of molecular vibration which is propagated from point to point at the rate of 28 to 30 metres to the second. This molecular vibration extends both ways along the nerve; when the stimulus is applied midway, its existence is evident only at the nervous extremity, where an organ suitable for its reception may be found; as, for instance, towards the central end for sensitive nerves, and at the surface or periphery for the motor nerves. Thus it may be noticed that the terms centripetal and centrifugal depend upon the different connections, and that both can conduct, indifferently, either way (Vulpian).

4. *Excitants of the Nervous System.*—Those excitants which can set in motion the functions of the nerves are numerous. Some of these are chemical, such as acids, ammonia, &c.; these agents, it will be seen, excite likewise the muscles, but in this case they need not be so concentrated as in the former. Others may be in the nature of mechanical or physical excitants; as, for instance, a blow, electricity or heat. Electricity seems to excite the nerves only by the sudden changes it produces in their molecular condition; thus a current applied to a nerve affects its action, only when it begins or terminates its passage through the nerve; during its passage no action is evident. In order to excite nerves, sudden electrical discharges must be applied, and this is the reason for the employment of an induced current, frequently interrupted. At each interruption, there ensues an excitation of the nerve. In normal physiological conditions, the external excitors are brought to bear upon the ends of the so-called sensitive nerves; certain of the peripheral organs of this class (organs of special sense) exist where particular agents (light, sound, heat, odors, &c.), give rise to special excitations.

Finally, the central organs act as physiological excitants in the reflex order, where they only transmit previously received excitations, and in the phenomena called voluntary (which are doubtless a more or less complex form of reflex actions). This is due to the power which the nerve globules possess of storing up certain excitations (memory), whose manifestations they allow only at a given time. We may perhaps

suppose that the central nerve globules, by the simple effect of their nutrition, and without excitation coming from outside the body, are capable of setting free forces which act upon the fibres; this property has been called automatism of the nerve centres (will, muscular tone?)

5. *Excitability of the Nerve Elements.* — The excitability of the nerve elements, especially if a nerve used for experimental researches, may vary under many circumstances. Heat increases this up to a certain point: cold diminishes it. Certain medicinal agents, as, for instance, strychnine, have the power of exciting the reflex properties of the nervous centres; others, like the bromide of potassium, enfeeble these properties. Woorara (*curare*), on the other hand, seems to act especially upon the motory terminations of the nerves, and there to arrest the power of transmission, for it is hardly reasonable to suppose that it would act upon the motory nerves, and not upon the sensory nerves; this would show that these two kinds of nerves have no different characters.

Electricity acts at the same time both as an excitant and as a modifying agent of excitability to a nerve; in fact, when a current is applied to a nerve, excitability is increased at the negative pole, and diminished at the positive pole, a phenomenon more especially described under the head of *electro-tonus*.

But the excitability of a nerve is especially dependent on its nutrition. Every nerve tube separated from a central living organ undergoes fatty degeneration and ceases to be excitable at the end of a few days. Absolute rest produces the same effect, for the function is necessary to the maintenance of life and of nutrition; *per contra*, the exaggerated excitations produce momentarily the weakening of a nerve, which must needs recover its strength by rest, and we have remarked that excitation of the nerve modifies temporarily the phenomena of nutrition.

II. General Physiology of the Nerve Centres.

For a long time the point of departure of the nervous system was a matter of ignorance: the size and position of the brain led the ancient physiologists to consider that as the principal centre of the nerve-substance: the spinal cord was to them but a collection of nerves ending at the brain. The minute study (histology) of the gray axis of the spinal cord

and the physiological experiments of Legallois lead us *now* to consider the spinal cord as the principal nerve-centre of the organism. Experimental researches have been principally concerned with the spinal cord, and the characteristics discovered here have been, reasoning by analogy, extended to other portions of the nervous system.

Nerve Centre, Gray Matter, Nerve Commissures. — In the actual state of our knowledge, the three principal objects in the central nerve masses are: the brain, the spinal cord, and the small nerve centres called *ganglia* (system of the grand sympathetic) distributed through the visceral cavities; these latter have slight, if any, connection with the brain. But the exact notions that we possess are applied almost exclusively to one of these objects; viz., the spinal cord and its encephalic portion (bulb, protuberance).

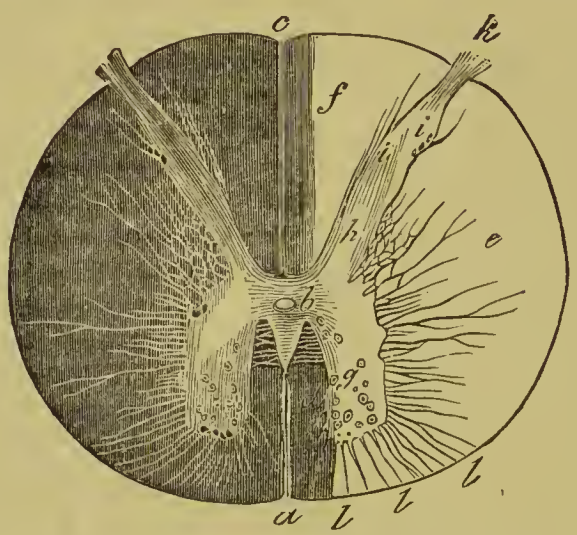


Fig. 11. — Transverse section of the spinal cord in man.*

From an anatomical point of view the central portions are characterized by the presence of nerve-cells; but from a physiological point of view they are characterized by the reflex act.

Nerve globules of the spinal cord form in this organ a central continuous mass (gray substance, gray axis) stretching from one end of the organ to the other. (Fig. 11.) But

* Cervical region (10 diameters). *f*, Posterior columns. *ii*, Gelatinous substance of the posterior horn. *k*, Posterior root. *l*, Anterior roots. *a*, Anterior median fissure. *c*, Posterior median fissure. *b*, Central canal of the cord. *g*, Anterior horns. *h*, Posterior horns. *e*, Antero-lateral column.

if anatomy places the upper bounds of the spinal cord at the point of the occipito-atloidean articulation, the physiologist extends the spinal cord to the interior of the cranium, as well as along the vertebral canal, and even as far as the *sella turcica*, where it ends with the pituitary body (bulb, protuberance, cerebral peduncles, gray matter of the third ventricle.) (Fig. 12.)

In the *encephalic mass*, properly so called, the nerve globules are distributed in isolated layers, and form a number of islets. These masses are placed above the cephalic extremity of the spinal cord, and form in this place series of transverse bands. Near the place where the spinal cord bends before terminating in the *sella turcica* are found a number of isolated little groups of globular matter. They form, in a manner, separated stages in the cranial cavity, and are placed in concentric layers one upon the other. (Fig. 12, D.) These stages have received different names; the most superficial of them is in contact with the skull, and appears in the form of an undulating surface enveloping the whole, and is called the cortical substance of the encephalon. (Gray substance of the cerebral convolutions. Fig. 12, E, E.) Between this and the encephalic prolongation of the spinal cord (A) are found: two important groups

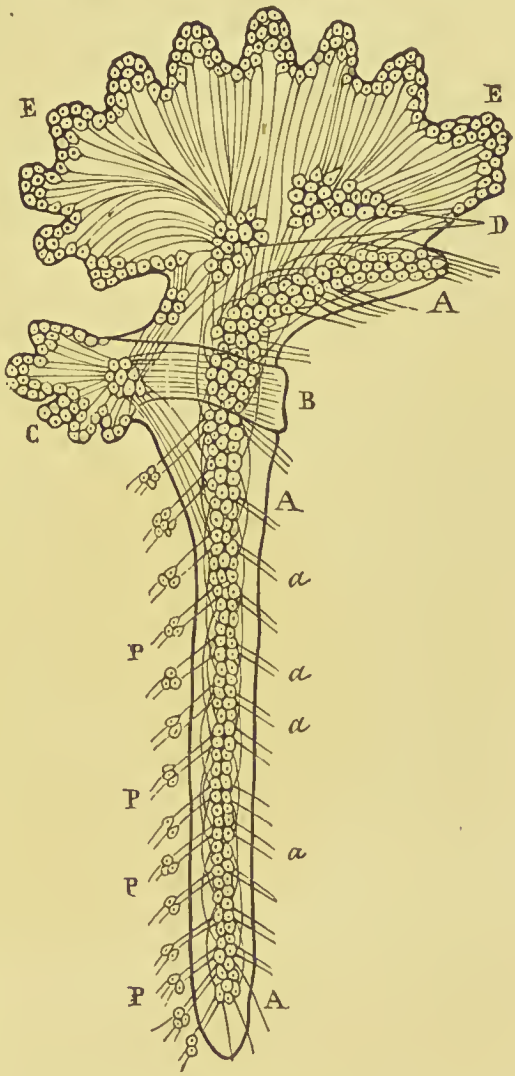


Fig. 12.
Plan of the central nervous system.

* A, A, A, Spinal cord, with its commissures. B, Region of the protuberance. C, Cerebellum. D, Thalami optici and corpora striata. E, E, Gray matter (cortical substance) of the cerebral convolutions. *a*, *a*, *a*, Anterior roots. P, P, P, Posterior roots.

(D), the *corpora striata* in front, and the *thalami optici* behind. Finally, in the posterior portion of the encephalic mass, the cerebellum reproduces on a small scale the preceding disposition. (Fig. 12, C. *Gray convolutions* and *rhomboid body* of the cerebellum.)

We know, moreover, that the prolongations start from the nerve globules, which thus unite them to each other; in this way a group of these prolongations form a communication in the brain between the superficial and the inner layer of the globules, thus constituting the *corona radiata* (*fibrous cone*); lying deeper the *thalamus opticus*, or the *corpus striatum*, uniting the middle with the lowest layer.

The same plan holds in the cerebellum. Collections of nerve prolongations stretch from one portion of the surface, or *cortical layer*, to the rhomboid body (*corpus dentatum*) of the cerebellum, then from the latter to the other portions of the encephalon and spinal cord (*pedunculi cerebelli*, separated into superior, middle, and inferior). In brief, the encephalon is a very complex system of little continents of gray or central nerve substance, intercommunicating with themselves and spinal cord by numerous commissures.

The spinal cord, likewise, presents similar commissures; but in this case they are generally longitudinal, and surround the gray centre of the spinal cord with an envelope of white substance (antero-lateral and posterior columns), and then make a communication from one globule to another in the spinal cord, and again between these globules and the brain mass.

Among these different globules of the centres there are no communications except with these commissures: they simply communicate with each other. There are other communications, placed outside of the nerve centres, with the peripheral parts, by means of nerves in the true sense of the word. The spinal canal (spinal or rachidian, and cephalic portions) alone seems to possess the property of establishing outside communications with the different organs of the economy. All the fibres to be met with in the cerebrum or cerebellum are doubtless real commissures, and only in an indirect way, by the mediation of the cord, can the peripheral nerves be made to accord with the encephalic centres, in order either to produce the sensations (centripetal nerves), or to bring into action the property of volition (centrifugal nerves).

III. Special Physiology of the Nervous System.

A. Peripheral nerves.

The physiology of the nerves which go from the brain to the spinal cord has been a very engrossing and laborious study; minute dissections, experiments on animals, pathological observations studied in man, have been alternately used to prove the functions of each nervous filament, and yet, especially for the cranial nerves, science has not yet accomplished any degree of desirable precision. We can only here briefly indicate the principal results of physiological researches, which, for the cranial nerves, can be understood only by an exact knowledge of the complicated topography of this portion of the nervous system.

1. *Cranial Nerves.* — The twelve nerves which originate from the encephalic portion of the nerve centres (base of the brain, protuberance, bulb) preside over the general sensibility or the special sensibility, or the movements of those parts to which they are distributed; they may preside over either one of these functions exclusively, or be composed of different fibres (mixed nerves), some of which are sensitive, others motor.

Olfactory Nerve (1st pair). — This nerve appears to preside solely over the special sensibility that produces the sensation of smells; we say appears, because Cl. Bernard has compiled a number of observations (and specially in the case of Marie Lemens), where the complete absence of the olfactory nerves, determined at the autopsy, was not marked during life by an absence of the sense of smell. Magendie often confounded the special sensibility of the functions of the olfactory nerve with the general sensibility that the trigemini furnish to the olfactory mucous membrane.

Optic Nerve (2d pair). — This is a nerve of special sensibility, and carries to the brain the impressions of light received by the retina (*vide* organs of the special senses); also, every excitation (section, compression, etc.) of the optic nerve produces no sensation of pain, but simply an impression of light. The incomplete decussation (*chiasma*) of the optic nerves seems to explain single vision when both eyes are used. Indeed, this arrangement is such that the left optic tract, for instance, divides at the point of the chiasma, so that both the right and the left optic nerve form the left halves of both retinæ (the outer half of the left retina and the inner half of the right retina).

An object placed at the right would thus be perceived solely by means of the left optic tract, if we bear in mind the points of the two retinæ upon which its image would be depicted (so-called theory of coincident points; for all the points of the left half of a retina, coincident points are found in the left half of the other, and inversely.) We shall see when studying the retina, that this explanation, originating with Wollaston, loses much of its importance in the consideration of clear or distinct vision where the two images of the object would be depicted on the macula lutea (yellow spot) of each eye.

The optic nerve conveys luminous sensations towards the *tubercula quadrigemina.*

Motor Nerve of the Eye (3d pair, motor oculi).—This nerve is solely motor; it affords movement to those muscles to which it is distributed, namely, to the levator palpebræ (elevator of the eyelid), the superior internal and inferior straight muscles, and to the inferior oblique; also by means of the motor rootlet which it furnishes to the ophthalmic (or lenticular) ganglion, this nerve innervates (furnishes nervous power) to the muscles of the pupil (constrictor) and of the choroid (apparatus for accommodation).

Thus when this nerve is cut, or compressed by a tumor, the following symptoms may be noted, and in this way, the physiology of the common motor nerve of the eye may be summed up, and *à priori* its anatomical distribution be deduced: 1st, Exophthalmia; 2d, Closing of the upper lid; 3d, External strabismus; 4th, Inability to rotate the eye when the head is inclined on the opposite side of that in which the lesion is situated, or, moreover, according to recent researches, when the vision is directed obliquely from above outwards, or to the external side of the body (Donders). There is, then, diplopia with images crossed; the image furnished to the diseased side is inclined from this side, and is placed higher up than the image furnished by the healthy side; 5th, Dilatation of the pupil; 6th, Inability to adapt the eye for short distances.

Patheticus (4th pair, nervus trochlearis).—This nerve innervates the upper oblique muscle; it presides over the movements of rotation and of oblique vision. When it is cut or pathologically destroyed, symptoms just the opposite of those we have noted as No. 4 (see above), in the paralysis of the common motor are observed.

Motor Oculi Externus (6th nerve).—This nerve inner-

vates the external straight muscle, and presides over the movements outwards; its destruction consequently involves an internal strabismus.

Trifacial (5th pair, or nervus trigeminus).—This nerve is composed (two roots) of centripetal (sensitive) and of centrifugal fibres (motory or secretory).

Certain fibres have been named trophic, but, as there is a good deal of discussion in regard to their existence, it is hardly worth while to consider these in this work; disturbance of nutrition (trophic) observed after section of the trifacial, as well as of many other nerves, is dependent on loss of sensation to external injuries (Snellen), or to vaso-motor disturbances (Schiff). These fibres are distributed through the three branches of the trifacial.

The *opthalmic* nerve (or first division of the fifth pair) presides over sensation in the skin of the forehead, of the root and back of the nose, of the upper eyelid, over the sensation in the conjunctiva, of the cornea, of the iris, and even of the retina (general sensibility by means of the central nerve of the retina). It furnishes secretory fibres to the lachrymal gland.

The *superior maxillary* nerve presides over sensation of the lower eyelid, of the cheek, of the wing or side of the nose, of the upper lip, of the nasal mucous membrane (general sensibility), of the teeth of the upper jaw, etc. It furnishes *secretory filaments* to the glands of these different regions, and particularly to the glands of the olfactory mucous membrane. The motor branches which it appears to send off are but fibres of reflexion that come from the facial by a very complicated path (large superficial petrosal of the vidian nerve).

The *inferior maxillary* nerve presides over the sensation of the teeth of the lower jaw, of the skin of the chin, of the lower lip, of the auriculo-temporal region, of the buccal and lingual mucous membrane; it moreover presides over the special sensibility of the anterior half of the tongue (sense of taste), and the lingual nerve (lingual branch of the fifth pair) is generally considered as the nerve of this special sense. Though the *chorda tympani* may be concerned in the sense of taste, yet in all cases, gustatory nervous filaments are sent off by the trifacial, but by a complicated path which is not yet settled by physiologists (Lussana, Schiff). This nerve furnishes motory fibres to all the muscles of mastication, some of which (masseter, temporal, pterygoids) elevate the jaw,

and others (mylo-hyoid and the anterior belly of the digastric) depress the jaw, perhaps, also, to the stapedius and to the internal muscle of the malleus; but these last-named filaments appear to be mostly branches belonging to the facial, as well as to the secretory, filaments, which go to the submaxillary, sublingual (chorda tympani), and parotid glands.

Summing up, it will be seen that the trifacial nerve essentially presides over the sensibility of the three grand divisions of the face (forehead, cheeks, and chin), whence the name trigeminus or trifacial.

Facial Nerve (portio dura of the 7th pair). — This is essentially a centrifugal nerve (motory and secretory); the secretory functions devolve apparently on the *intermediary nerve of Wrisberg* (Cl. Bernard). The facial receives some sensory anastomoses which proceed to it from the pneumogastric and trifacial nerves.

By its terminal branches this nerve presides over the movements of all the cutaneous (*peauciers*) muscles of the head, from the frontal to the occipital, comprising among these the buccinator, and even to the cutaneous muscle of the neck. Through its filaments, whose path is as complicated as the windings of the aqueduct of Fallopius, whose canal it follows, it presides over the secretion from the different salivary glands, the contraction of the muscles concerned in the first intervals of deglutition (velum palati, styloid muscles, posterior belly of the digastric, etc.), as well as the contractions of the muscles of the middle ear (tensor tympani, or musculus internus mallei, and stapedius). Longet regards the branches given off to these last two muscles as being the continuation of the *intermediary of Wrisberg*, which he names consequently *motory tympanic nerve.*

By the above physiological notions, it is explained why paralyses of the facial nerve, arising from superficial causes, are characterized only by distortion of the features, whilst those from deep-seated causes involve, in addition, a certain difficulty of deglutition (deviation of the uvula, etc.) as well as of hearing.

Auditory Nerve (portio mollis of the 7th pair). — This is the special nerve of the organ of hearing. Its irritation can only occasion sensation of sounds; its section is followed by complete deafness. Its partial section in experiments on animals cause movements of rotation (Flourens) that have been explained as caused by a vertigo of the senses (Gratiolet, Vulpian).

Glosso-pharyngeal Nerve.—This is a mixed nerve even from its origin (Mueller, Bernard); however, Longet considers this primarily a sensory nerve, possessing no derived motor filaments. If experiments on animals do not always allow of the determination of motory properties (Jolyet), still the existence of these can be deduced from the rapidity with which these lose their power of excitability (Biffi, Morganti, Schiff). The glosso-pharyngeal presides over the movements of the pharynx, (as also the facial, pneumo-gastric, and spinal), over the general sensibility of the region of the fauces, of the base of the tongue, and finally over the special or gustatory sensibility of the base of the tongue (see organs of special sense, taste).

Pneumo-gastric (nervus vagus, par vagum).—Bischoff and Longet are unwilling to admit in the roots of this nerve any other than sensory filaments; still experiments by Bernard, Van Kempen, Vulpian, and Jolyet prove that the pneumo-gastric is both motory and sensory, from its origin; it is also true that it receives a large number of motory anastomoses from the neighboring nerves.

The very complicated physiology of this nerve, taking into consideration its very complex anatomical distribution, is found to vary with each organ to which its branches are sent off (see circulation, digestion, and respiration). We can here only generalize upon these functions. The pneumo-gastric might be called a mixed tri-visceral nerve, or, in other words, it affords sensibility and movement to three great viscera (heart, lungs, and stomach), and also to their appendages. But it must be remembered that the sensibility afforded by this nerve is generally obtuse, and in no wise localized, and gives vague sensations of the kind called general (see farther on; physiology of the encephalon), or may give rise to reflected actions of which the mind is unconscious. Consequently the movements over which it presides are mostly reflex, and but slightly under the power of the will.

In the apparatus for respiration, the pneumo-gastric affords sensibility to the glottis, the trachea, and the lung (the centripetal conductor of the desire of breathing); also motion to the glottis (movements of respiration and not of phonation. Cl. Bernard); also to the smooth, muscular fibres of the trachea and bronchi (Williams, Paul Bert).

In the central apparatus for circulation, it gives sensory and moderating cardiac nerves (see circulation).

In the digestive apparatus, it furnishes sensibility to the pharynx, œsophagus, and stomach, as well as motion to these same parts, and perhaps, also, to the small intestine.

[According to Legros and Onimus, electrization of the pneumo-gastric, with interrupted currents (faradization), arrests intestinal movements, and arrests these not in a state of contraction but of relaxation.]

Finally, it presides over the secretion of the glands of the trachea and bronchi, and perhaps, also, the glands of the stomach; however, in this connection, the experiments are contradictory and even less conclusive concerning these last-named points; the same holds true with regard to the formation of sugar in the liver; these fibres, according to Cl. Bernard, seem to be centripetal; by means of their peripheral extremities located in the lungs they would excite reflexively those nerves tending to the formation of sugar (vaso-motor?).

Spinal Accessory Nerve.—This, considered by Bischoff and Longet as accessory (motory portion) to the pneumo-gastric, is, in a physiological point of view, the especial antagonist of the pneumo-gastric, since it presides over the movements of phonation, almost all of which are opposed to the respiratory movements, strictly speaking, as well in the glottis (internal branch of the spinal nerve) as in the thorax (external branch) (Cl. Bernard). Special indications are also found in the study of phonation, which lead to the consideration of the spinal as a *nerve of phonation and of mimicry.*

Hypoglossal (9th pair). — This is exclusively a motory nerve for the tongue and hyoid muscles. When this nerve is cut in a dog, the animal can no longer move his tongue, which hangs out between the teeth; he bites the tongue when moving the jaws, and seems to feel acute pain from the wounds, but is powerless to withdraw the tongue behind the dental arches.

2. *Spinal Nerves.* — The thirty-one pairs of nerves given off from the spinal cord form mixed roots, and contain an inextricable mixture of centripetal and centrifugal nerves; however, these two elements, so opposing in character, are for a short distance separated, and called by the name of the spinal roots.

The *anterior roots* (Fig. 13, A, A, A) contain centrifugal fibres, that is to say, secretory and motor nerves, destined as much for the striated as for the smooth muscles (among others, the vaso-motor apparatus).

The *posterior roots* (Fig. 13, P, P, P) contain centripetal or sensory fibres.

This exact explanation of the function of the spinal roots has been generally attributed to Charles Bell, but to-day it is admitted that the glory belongs to Magendie (Vulpian). This discovery has been the point of departure in all our modern conquests in the physiology of the nervous system.

Though the anterior roots possess also some sensory fibres, these fibres are sent off to them from the posterior roots. These are the *recurrent fibres*, and from this fact has arisen the idea of recurrent sensibility (Magendie, Cl. Bernard); in fact, these sensory fibres follow, in their progress to the spinal cord, the anterior roots from centre to periphery, and then, either at the anastomosis of the two roots, or, more probably, at the point of the plexus (cervical, thoracic, lumbar, etc.), they turn back towards the posterior roots, entering with them the medullary centre. The recurrent sensibility of the anterior roots is then no exception to the general rule; all in these is centrifugal, all in the posterior roots centripetal. So, when an anterior root is cut, the peripheral end only is still sensible. This experiment is a most complete demonstration of recurrent sensibility, especially when we observe that immediate disappearance of this recurrent sensibility in the anterior root is caused by section of the posterior root.

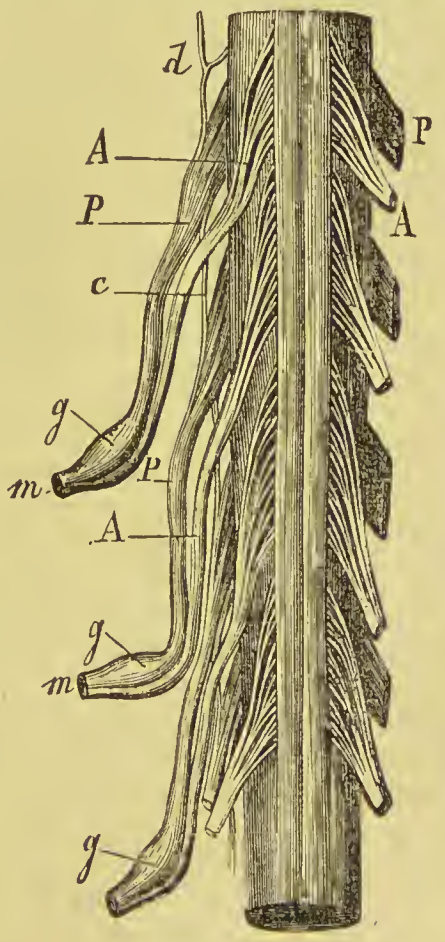


Fig. 13.
Origin of the spinal roots.*

In the course of each posterior root, a little before the

* The anterior surface of the cord is here shown. A, A, A, Anterior spinal roots, with separate origins, uniting afterwards to form the plexus of the root. P, P, P, Posterior roots. *c*, *d*, Anastomotic filaments sometimes found between the posterior roots. *g*, *g*, *g*, Ganglions of the posterior roots. *m*, *m*. Mixed nerves, formed by the union of two roots.

point of junction of the two roots, is placed a small ganglion. This ganglion is made up of a collection of cells having the most different and ill-defined relations with the nerve tubes distributed in it. We do not know the functions of this ganglion; we only know that it plays some part in nutrition (*rôle trophique*), as discovered first by Waller, and since confirmed by Bernard and many other physiologists. When an anterior root is cut, the peripheral or distal end is disorganized, whilst the central end is uninjured, because it is still connected with its own trophic centre, namely, the spinal cord. On the other hand, when a posterior root is cut between the spinal cord and the ganglion, the end remaining in connection with the ganglion remains intact, whilst the

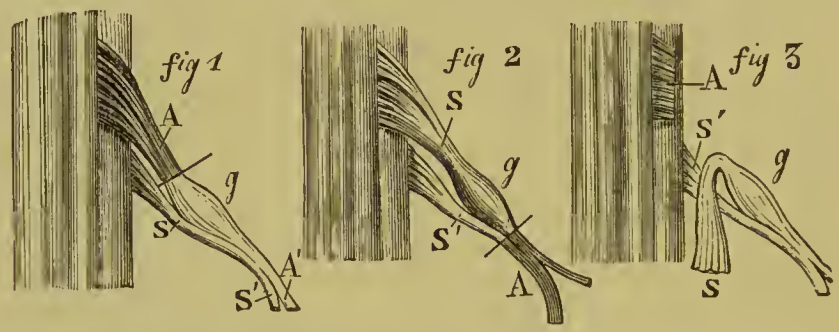


Fig. 14. — Changes produced in the nerves by section of the spinal roots.*

end fastened to the spinal cord is disorganized (Fig. 14, 1 and 3); the ganglions of the posterior roots possess, then, the property of trophic centres of those roots connected with them, or, in other words, of the sensory nerves. Indeed, there is no need of mentioning that if the mixed nerve (root?) be cut beyond the ganglion, all the peripheral or distal portion is altered, — the sensory elements as well as the motory elements (Fig. 14, 2).

B. Spinal Cord.

1. *Means of Conduction.* — The *centripetal* nerves return, then, to the spinal cord by the posterior spinal roots; having

* Fig. 1. The section is made in the posterior root, above the ganglion. The portion A, comprising that between the section and the cord, alone undergoes any change; the portion A, extending to the ganglion *g*, remains unchanged, as well as the anterior root S.

Fig. 2. The section is made of the mixed nerve, immediately below the junction of the two roots. The portion A of the mixed nerve is changed, the two roots (the posterior S and its ganglion *g*) remaining unchanged.

Fig. 3. The posterior root is separated from the cord at A. Its peripheral extremity S (turned down) undergoes no change. (Cl. Bernard.)

taken more or less part in the formation of the white posterior columns, they then join the gray substance. Thus it may be said that sensibility traverses the posterior roots, the posterior columns, and the gray substance: this last seems more particularly endowed with the conduction of *painful sensations*, and the posterior columns to the sensations of touch or contact. In fact, by experimentation each of these modes of sensation can be destroyed, and they are perfectly isolated by the state of chloroformization (or etherization). An animal whose gray axis alone has been bisected, or which has been subjected to the action of chloroform, loses sensation of pain, but yet all the tactile sensations may be carried to the brain. The centrifugal nerves form the antero-lateral columns, and then leave the spinal cord by the anterior roots of the spinal nerves; these roots start from the gray substance of the cord. So the white substance of the cord is formed by the nerve roots that go through this spinal cord in a more or less oblique direction, and also by vertical fibres (properly called *columns*), the whole enclosed in a peculiar uniting substance, which German histologists consider to be the embryonic form of the connective tissue.[1]

The knowledge of the centrifugal functions of the antero-lateral column and of the anterior roots, of the centripetal functions of the posterior roots and of the posterior columns, form the essential points of the physiology of the spinal cord; but in order to satisfy the demands of pathology, and for an explanation of the numerous facts discovered by vivisections and the study of the degenerations of the fibres of the spinal, physiology should seek for a solution of the following questions: What is the object of the connective tissue in the structure of the spinal cord? What is the direction of the fibres of the roots? Do these go directly to the encephalon, or do they terminate in the cells of the spinal cord? Are the fasciculi of the cord as excitable as the nerves? Do these follow an ascending or descending course, or do they cross from one side of the cord to the other?

Neuroglia, a kind of connective tissue in the spinal cord, adopting the explanation of Virchow (op. cit. pp. 71, *et seq.*) has been the especial study of anatomists belonging to the school at Dorpat, who, moreover, have perhaps slightly exaggerated its importance (Owsjanikow, Metzler, Kupffer,

[1] Neuroglia, or nerve cement. Virchow's "Cellular Pathology," translated by Chance, Am. ed., p. 315.

Bidder, etc.). They consider it composed of a connective meshwork (neuroglia) formed of trabeculæ which may be compared with the meshes of a sponge, and in certain places it may even be condensed; as, for instance, 1st, in the periphery where it forms a *cortical envelope;* 2d, around the central canal of the spinal cord (periependymal nucleus) (see also, Virchow, op. cit. p. 312); 3d, upon the two sides which limit the posterior median fissure (septum posticum of Goll); 4th, around the posterior horns, where it forms the gelatinous substance of Rolando, so well studied by Luys.[1] The essential part of this tissue in pathological *neoplasms* (new formations) explains the importance attached to its study.

With regard to the *course of the nerve fibres* in the spinal cord, we have already insisted in this connection (*vide* p. 34) that the spinal cord is principally a *commissure* between the encephalon and the peripheral nerves, and indeed vivisections, and especially the study of degenerations in the spinal cord after section performed experimentally, or after pathological alterations, have proved: 1st, that the posterior roots are almost immediately lost sight of in the posterior horns of the gray substance, some by their horizontal course, others in an oblique course more or less upwards or even downwards; some globules of the posterior horn start off then from fibres which mount in the posterior columns even to the floor of the fourth ventricle, and perhaps some may extend even as far as the encephalon (L. Turck). The rest of the posterior columns is formed of commissural fibres which unite one region of the posterior horns to another of those horns situated either above or below. 2d. The anterior roots start from the anterior horns, and traverse almost in a horizontal direction the white antero-lateral fasciculus; this fasciculus is formed of fibres coming from the *corpus striatum* in the anterior horns, and by some vertical commissures from one portion of these horns to another situated either above or below. (Fig. 12.)

The *excitability of these fasciculi* of the spinal cord forms a problem difficult of solution, and upon which physiologists are far from agreement. 1st. The antero-lateral column is considered inexcitable by most physiologists; however, Longet has often obtained movements by the application of

[1] J. Luys. "Recherches sur le Système Nerveux Cérébro-spinal." Paris, 1865. Luys considers that this substance is formed of nerve elements, and not of connective tissue.

electricity to these columns; more recently Fick has arrived at similar results, and, moreover, has found that these columns respond to mechanical irritations (pinching or bruising). We shall conclude, then, as has this last-named experimenter, that the excitability of the white anterior columns is real, though less intense than that of the corresponding roots; destined to transmit the commands of volition, these cerebro-spinal commissures are not set in action except under the influence of mechanical agents of sufficient energy. 2d. All physiologists from the time of Magendie recognize that the posterior columns are directly excitable by irritants more or less slight, and then originate painful sensations. Movements of a reflex character are likewise produced. 3d. Finally, in order no longer to revert to these facts of excitability, let us remark that the gray axis of the spinal cord is universally recognized as inexcitable.

The *decussation* (crossing over) *of the columns of the spinal cord*, now perhaps admitted as a general fact, has been for a long time suspected (Galen). Experiment has shown that this decussation occurs in the different columns as well as in different parts of the same column at various points: 1st, the antero-lateral column is but little, if at all, the seat of decussation throughout the length of the spinal cord properly so called; this decussation occurs at the point of the bulb (*decussation of the pyramids*), but in the innermost band of the anterior columns there is none; the decussation of this column occurs higher up: in every case there is found in front of the protuberance new decussations of fibres, and especially nerve fibres that go from the brain to the roots of the nerves of that region (facial, motores oculorum); in treatises on pathology it will be remarked how a knowledge of these decussations are an important means of explaining paralyses on the side of the face and extremities opposite the lesion (Gubler). 2d. According to the majority of physiologists, the posterior columns decussate throughout the length of the spinal cord, in such wise that the unilateral lesions of the spinal cord destroy sensibility on the opposite side and motility on the same side as that in which they occur. 3d. Finally, in the gray substance, which also serves as a conductor, there seems to be a decussation, but here the facts are less distinct; the transmission of sensibility appears in every way, for if two transverse semi-sections are made at different heights of the spinal cord, the transmission of peripheral (or outward) impressions is not interrupted; provided

there may be a bridge, however small, between the gray substance of the right and that of the left, peripheral impression can be perceived, and thus pain be caused (indifferent transmission, Stilling, Vulpian).

Brown-Séquard has even gone further in the analysis of special conductors composing the columns of the spinal cord; according to him there are more numerous and even more distinct conductors of sensibility than have been generally supposed. Basing his opinion upon clinical observations of anæsthesia, hyperæsthesia, and of special subjective sensations, he allows special conductors for the sense of touch, tickling, temperature, and of pain; all these conductors are situated in the posterior columns and intercross or decussate in such a manner that every portion of the conducting zone in a posterior lateral half of the spinal cord contains conductors coming from every point of the opposite side. Besides these four conductors contained in the posterior columns, Brown-Séquard notices three others which form the antero-lateral columns, and pursuing a direct course (at least in the spinal cord); these are the conductors of voluntary movements, vaso-motors, and conductors of the muscular sense (!); these constitute a sum-total of seven special conductors comprised in the spinal cord.

2. *The Spinal Cord as a Nerve Centre; Reflex Centres.* — Up to this point we have considered the spinal cord only in the light of a conductor; but we have mentioned before in the general study of nerve centres (*vide* p. 32) that, judging from modern investigations, the spinal cord should be considered the principal one of these centres. The globules of the gray matter of the spinal cord establish in a more or less direct manner the functional connection between the centripetal fibres which go towards this centre, and the centrifugal fibres which go from this centre; hence they preside over the reflex actions.

So the gray matter of the spinal cord suffices for the transformation of sensibility into movement, and most often it does this without the intervention of the cerebral function. If a section of the spinal cord be made below the brain, the peripheral portions by this interference cease from being in communication with a reflecting nerve centre; and yet in such an instance a movement of the extremities may be provoked, as for example by tickling the bottoms of the feet. This same fact is also observed in certain paralyses, where, in spite of alterations of the upper part of the spinal cord, a

shock, cold, tickling, and other excitants of the centripetal nerves, will produce movements as well as secretions.

Reflex Movements. — The spinal cord can also produce certain very complicated reflex movements with assistance of the brain; of this kind are the movements of defence that are observed in those decapitated animals who may be subjected to irritations (frogs or tritons). Most generally the movements of progression (walking, leaping, or swimming) are made without the intervention of intellectual action; volition can be completely unconcerned in the process of walking, and we ordinarily walk without knowing it, as we might say. This phenomenon is the act and even the exclusive act of the spinal cord. The brain is concerned only at certain times, when, for instance, we desire to regulate the speed either by retarding or hastening our step.

From the moment it is admitted that all organic acts are the result of a peripheral impression, all these acts have a reflex character; thus all organs present in the study of their functions a series of reflex acts in which we shall see the spinal cord acting, not as auxiliary to the brain, but as a true centre, which in certain cases can act for itself alone. A few examples of reflex acts will help us more clearly to understand the method of the function of the nerve centres and of the spinal cord in particular.

Sneezing is a phenomenon provoked either by an excitation brought to bear on the nasal mucous membrane or by a sudden shock of the sun's rays on the membranes of the eye. This peripheral irritation is transmitted by the trifacial nerve to the Gasserian ganglion, whence it passes by a commissure to an agglomeration of globules in the medulla oblongata or in the protuberance; from this point, by a series of numerous reflex and complicated acts, it is transformed by the mediation of the spinal cord into a centrifugal excitation which radiates outwards by means of the spinal nerves to the expiratory muscles.

The respiratory movement depends on the spinal cord. This presides over the regularity of respiration; in order to set up this reflex phenomenon the sensitive surfaces of the trachea and of the pulmonary vesicles (air cells) must receive an impression from the introduction of external air, or by air vitiated and loaded with carbonic acid following the pulmonary gaseous exchanges.

The *movements of the heart* are the result of analogous mechanism; these are possible only when the internal surface

of the heart is in direct contact with the blood. This contact plays the part of a peripheral impression. If it were possible to empty the heart completely of all the blood that it contained, it would stop its pulsations until a few drops of blood should be introduced, after which its movements would continue; however the nerve globules that preside over this reflex act are situated in the thick walls of the heart (See circulation).

Walking is also, as we have already said, a reflex phenomenon; its point of departure is the peripheral impression produced by the contact of the foot with the ground. The sole of the foot is plentifully supplied with tactile apparatus. If this peripheral impression be but imperfectly transmitted to the nerve centre, reflex action has no longer any regularity. Thus when the great sciatic nerve has been compressed in certain postures, during the few moments it remains paralyzed (for sensation only) walking becomes impossible or at least painful.

There are other examples of reflex action fully as important as the preceding, principal among which are the secretions. It is generally admitted as a rule that previous to every secretion a peripheral impression is transmitted to the nerve centres and thence to the gland. The salivary secretion is dependent on the centripetal nerves of taste which convey the impressions of taste to the medulla oblongata, whence they are reflected by means of the centrifugal nerves (facial) to the glands and their vessels. These centrifugal nerves seem to act directly on the cells of the secretory organ, independently of the vascular elements; for if the circulation in a gland be suppressed simultaneously with the excitation of its functions, it affords to the surrounding tissues the materials no longer furnished by the blood and the gland continues to secrete. The secretion of gastric juice might be cited as an example of the reflex action of whose existence we are unconscious; but in this connection is presented the peculiar fact, that the secretion must be provoked by a suitable excitant, an *aliment* (we shall mention at another time that the introduction of foreign bodies, small pebbles, in the stomach provokes no secretion of true gastric juice, but of a mucus possessing no digestive properties).

We have remarked that, in the eyes of the physiologist, the spinal cord extends as far as the sella turcica. This view is sustained by the study of reflex actions whose centre is in the cranial portion of the cord; there, as well as in the spinal

portion, we find masses of globules serving as reflecting centres, transforming the sensory impressions into motor effects; moreover these centres are better defined and their irradiations more localized than those in the proper spinal cord.

In the cephalic region there are found a series of centres beginning low down and going upwards (or from behind forwards), for whose exact determination modern physiological investigations are especially applied; we shall only now cite the example of a few of the most important, as these centres will be more exactly pointed out, as well as their centripetal and centrifugal nerves, when the different functions over which they preside are considered.

In the bulb is found: the centre of deglutition; — of the movements of mastication; — expression of imitation; — of speech (olivary bodies, according to Schroeder van der Kolk, and Duchenne, of Boulogne: consequently, in this centre should the cause of those singular paralyses, known by the name of *labio-glosso-pharyngeal*, be sought); — the centre of respiratory movements: this centre is composed of a little mass of gray substance situated towards the point of the *calamus scriptorius* (floor of the fourth ventricle), this is the *point* or *vital knot* (Flourens, Longet), so-called because its lesion causes in cold-blooded animals an instantaneous death, and this simply by an immediate arrest of respiration (see respiration, influence of oxygen and carbonic acid upon the respiratory centre); — the centre of cardiac movements (moderating fibres of the pneumo gastric); — a portion of the vaso-motor centres (Ludwig, Thiry).

At the protuberance, and as high up as the cerebral peduncules, are found: another portion of the vaso-motor centres (Tcheschichin); — the centres of *innervation of the movements of locomotion:* these last-named centres appear to be in communication with the different encephalic centres, properly so called, which are attached to the protuberance by peduncles (middle cerebellar peduncles and cerebral peduncles). Lesions of these peduncles occasion a disturbance in the coordination of movements; unilateral lesions give rise to the peculiar movements of rotation, which occur under the form of whirling (a continuous motion around some imaginary central point), or of motion on a pivot (the posterior portion of the animal remains fixed whilst the anterior portion revolves around the former as a centre), or of a rolling motion (rotation around the longitudinal axis of the body), or of somersaults (sudden movements forwards or backwards).

Finally, the protuberance and the cerebral peduncles comprise in addition *motor-centres for the movements of the globe of the eye* (eyeball, etc.).

If a study of the reflex centres situated in front of or above the before-named centres is begun, new phenomena complicate the inquiry: these are phenomena of *perception*, or of *volition*, so-called, which will be studied with the cerebral centres, properly so called; but even at the level of the protuberance we shall have to admit phenomena of *perception*, and we shall see that this is one of the principal seats of the *reception of sensations*, but not of their *conservation* under the form of *memory*, and of their awakening under the form of *ideas*. So the physiological separation between the cephalic portion of the spinal cord and the cerebral organs, strictly speaking, is not perfectly distinct, and we cannot in fact designate the protuberance as the seat of transition, as a point half-way between the spinal cord, explanation of whose functions is relatively so easy, and the brain, which presents so much more mysterious phenomena.

To sum up, the *reflex act* will be always the fundamental fact in the functions of every nerve centre; it may be understood, then, why so much attention is paid to the reflex actions, their classification, the discovery of influences that can exaggerate or diminish them, and that this study should be principally occupied with the spinal portion of the cerebro-spinal axis where the reflex action by means of experimentation is easily isolated from all phenomena which could complicate it. We can merely pass rapidly in review over the results obtained by this study, which commenced only at the close of the last century.

The word *reflex*, or *reflection*, applied to certain nervous phenomena, was first used by Astruc (1743), who sought to explain the functions of the brain, and particularly the motor-reactions which follow a sensory impression, by a sort of *reflection* of the latter striking against the *columns of the brain* and being reflected like a luminous ray from a polished surface. The comparison was well made to illustrate the method of study of the reflex phenomena, but applied to the brain itself could lead to no result, for in the latter these phenomena are too complicated. It was only by following the researches of Robert Whytt, Prochaska, and Legallois, upon the spinal cord, and upon that which is called the *sensorium commune*, that Prochaska himself was able to distinctly indicate both the principal seat (spinal cord) and the substance

also of the phenomena which then took the name of *reflex* (*impressionum sensoriarum in motorias reflexio*) (1784); finally the histological study of the nerve globule, and its relations with the elementary fibres, afforded an opportunity of making a more exact account of the mode by which this reflection is made, though in regard to this latter point most of the facts are even yet quite hypothetical. Since that time Marshall Hall, Mueller, Lallemand, Flourens, Longet, Cl. Bernard, etc., have enriched science with facts numerous enough to allow of the *classification* of the reflex actions, of laying down the precise laws of their production, as well as the influences that modify them (especially in regard to the medullary reflex actions).

Classification of Reflex Actions. — These are divided according to the direction followed by the centripetal and centrifugal actions: these actions present two directions; either the nerves of the cerebro-spinal system, which have occupied our attention up to this point, or the branches of the great sympathetic, which will terminate our study of the nervous system.

The most numerous of the reflex actions follow the centripetal and centrifugal direction of the spinal nerve filaments; of this class, the larger portion we have already cited under deglutition, sneezing, cough, walking, etc., and in pathology a large number of morbid reflex actions, as vomiting, tetanus, epilepsy, etc.

A second class, almost as numerous, comprises those reflex actions where the centripetal direction is in the course a sensory nerve of the cerebro-spinal system, and the centrifugal direction a motor-nerve of the great sympathetic, most often a vaso-motor nerve; of this class are the reflex actions which give rise to most of the secretions (saliva, gastric juice, etc.), to the phenomena of blushing, or pallor of the skin, to erection, to certain movements of the iris, to certain modifications in the pulsations of the heart, and in pathology to a large number of phenomena called *metastatic*, on account of the great difficulty of accounting for the mechanism of their production, as for instance a large number of ophthalmias, of orchitis, of coryza, which depend on a reflex hyperæmia; and, on the other hand, dependent on a reflex anæmia, as, for instance, certain cases of amaurosis, paralyses, paraplegias, etc.[1]

[1] *Vide* Ch. Rouget, Introduction to "Diagnostic et Traitement des diverses espèces de Paralysies des Membres Inférieurs." By Brown-Séquard. Paris, 1864.

A third class comprises those reflex actions whose centripetal action is seated in the nerves of the sympathetic (obtuse sensibility, called *organic* in the viscera), and whose centrifugal course is that of the cerebro-spinal motor nerves (vital relations); most of these phenomena belong to pathology; of this class are convulsions, which may be caused by visceral irritations produced by intestinal worms, reflex eclampsia, hysteria, etc.; as a normal phenomenon of this kind, the respiratory reflex action may be cited, for the impression that the pulmonary surface sends to the bulb is transmitted by the pneumo-gastric; which, under favorable circumstances, is brought into relation with the nerves of the great sympathetic, or, at least, forms a physiological passage between the branches of the great sympathetic and those of the cerebro-spinal system.

Finally, a fourth and last class can be formed of reflex actions whose ways of centripetal as well as centrifugal conduction are found in the filaments of the great sympathetic; we shall have to examine at another time whether the central action for this class is located in the masses of gray matter of the cerebro-spinal system, or in those of the ganglions of the sympathetic chain; of this class are the obscure reflex actions and those which preside over the secretions of the various intestinal fluids that are still difficult of correct analysis; also those which can partially explain to us the sympathies that unite the various phenomena of the genital functions, especially in the female; also the dilatation of the pupils from the presence of intestinal worms in the digestive tract; and numerous reflex pathological actions analogous to those already spoken of.

Laws of Reflex Actions. — When a sensory impression causes a reflex phenomenon, the production of this latter is subjected in its intensity and anatomical distribution to certain precise rules, that Pflüger first established by experimentation on frogs (laws of Pflüger), and that Chauveau has confirmed by his experiments on the great mammalia. Thus a feeble irritation produced on the skin of the hinder extremities (for example, on the right side) causes a reflex movement in the muscles of the same extremity, that is to say, in the muscles whose motor nerves start from the spinal cord of the same side and at the same height as the sensory fibres which have been excited (*law of unilaterality*); if the excitation becomes more intense, the motory reaction is manifested on the opposite side, in the corresponding extremity: that is to

say, by means of the symmetrical nerves (*law of symmetry*); and this corresponding extremity (left, in the example selected) presents always movements less intense than that (right) which received the excitation (*law of intensity*). Finally, if the excitation still increases, the motory reaction is extended to the centrifugal fibres of a different height, but always advancing towards a higher (or anterior) portion of the spinal cord, that is to say, that the radiation extends from below upwards, from the spinal cord to the encephalic cord (bulb, protuberance, etc.), (*law of radiation*); lastly, if the excitation and consequently the motor-reaction are sufficiently energetic to be propagated from below upwards to the bulb and protuberance, the reaction becomes general, is propagated in every direction, both downwards and upwards; in such a manner that all the muscles of the body take part in it, the bulb acting as a general focus whence radiate all the reflex movements (*law of generalization*).

The reflex movements, obeying the five above-named laws, present, moreover, the remarkable fact that they are produced with a regularity, a co-ordination, which seems to indicate that these reflex actions are adapted to a certain purpose or aim; it appears as if there were in the histological dispositions of the spinal cord a *pre-established mechanism*, the manifestations of which so strongly impressed the first vivisectors, that they (Robert Whytt, Prochaska, Legallois, Pflüger) did not hesitate to endow the spinal cord with certain psychical properties, so vague and ill-defined, that they were designated under the name of *sensorium commune*, *volition*, *perception*, *soul* (the latter must not be confounded with the ecclesiastical name "soul"), etc.

Thus a frog whose brain had been removed (to eliminate every influence foreign to the spinal cord), reacted when the foot was pinched, as if to defend himself; if the skin of one of his extremities was cauterized by a drop of acid he would wipe it off with his foot, if perchance the acid had been placed upon the bend of the thigh or on the pelvic integument; moreover, if the leg which was bent thus towards the thigh were amputated, the animal, reduced to his medullary centre, was seen, after useless and droll efforts to reach the injured part (*law of unilaterality*), if the irritation persisted and especially if it increased, to use the limb of the opposite side (*law of symmetry*) and rub or wipe the part irritated. Should the irritation continue he would execute movements with all his other limbs, a forward jump, in fact a flight. Reflex

movements of this kind, though less perfect, are performed by man during sleep, when the cerebral organs are passive, and when the fact of tickling the sole of the foot is followed by a sudden withdrawal of the corresponding leg, or of both legs, etc. From this it may be remarked that the greatest number of reflex actions in co-ordination partake of the nature of defensive movements.

Variations in intensity of the Reflex Actions. — Whatever may be the phenomena which take place in the centres of the gray matter (nerve globules) at the time of the production of a reflex action, it is distinguished by the name of *reflex power*, or the property possessed by the gray axis of the spinal cord (or similar centres) of transforming centripetal impressions into centrifugal reactions; this expression seems to present a certain convenience of language, for it relates to agents that appear to convey their action upon the *reflex power*, either to diminish or increase this, without in any way acting upon the centripetal or centrifugal portion of the act, but solely upon the central act. We can here call to mind numerous investigations, by means of which the central action of these agents can in this way be precisely fixed, and we can distinguish among them analogous agents which convey their action upon the peripheral paths; a recollection of the beautiful experiments of Claude Bernard with woorara (*curare*) on the motor nerves (*vide* physiology of the muscles, muscular irritability). In connection with the agents that modify reflex power we will cite as examples: —

The surrounding temperature: reflex actions are more energetic and easier to provoke in summer than in winter (Brown-Séquard, Cayrade), but yet reflex power is rapidly exhausted during warm weather; — sections of the spinal cord or its separation from the encephalon: in these cases the reflex actions are exaggerated, which seems to be due to an irritation of the centres even from the act of the section, rather than to the interruption of all communication between these centres and other *centres* called *moderators* (Setschenow); and indeed this exaggeration of the reflex power after sections lasts but a short time; — a certain number of poisons convey their action directly upon the centres and exaggerate the reflex power; among these are strychnine, morphine, picrotoxine, nicotine, veratrine, cicutine, and certain pathological products of the organism, as in the septic infections (septicemia), uremia, severe icterus.

On the other hand, reflex power is diminished by anæmia,

by numerous successive irritations which weaken it, and by certain toxical or medicinal agents as hydrocyanic (prussic) acid, bromide of potassium, atropine, etc.

C. Encephalon.

General Functions of the cerebral or encephalic Centres properly so called. — By generalizing the expression *reflex phenomena* we can apply it to the phenomena which occur between the spinal cord and encephalon; in fact, the brain does not appear to communicate directly with any portion of the periphery, and can only perceive that which goes on in the spinal cord; thus in the brain infinite reflex actions occur between the numerous centres that are united by numerous commissures; and, in those phenomena which are considered *voluntary*, the brain reacts upon the spinal cord and thence outwards, in accordance with that series of actions which constitute the *perception* or *ego*.

Sensations. — The brain is then the seat of the interior phenomenon of *perception*, under the influence of an external agent whose action is transmitted to it by means of the peripheral nerves and by the spinal cord. Indeed perception is not produced during sleep, at which time the brain is at rest: but in speaking of the *brain* we should include, in the view of sensations, the whole encephalic mass and not merely its superficial layers, as a large number of acts attributed to perception seem to take place at the protuberance (see before, p. 50); so also a portion of the hemispheres and cerebellum can be removed without thereby causing the loss of sensation.

The phenomena of perception are divided into those which give us precise information of external objects, such as *special sensations*, which we shall refer to under the head of organs of special sense; and those called *general sensations*, which warn us only of those modifications that our organs undergo, without giving us precise information of the nature of the agents producing these modifications; pain is the special type of this latter kind of sensations. Intermediate between these two kinds of sensations have been placed those called *subjective* and *objective*.

The general or subjective sensations can also present two phases: in the first, the sensation (pain, for instance) is perfectly localized, as the sensation of a burn upon the skin; in the second form, on the contrary, the sensation is vague and difficult to localize; as the general *malaise* that marks the

commencement of asphyxia. Some have endeavored to express this difference by applying to the latter form of sensation the name of *sentiment*, and reserving for the former that of *sensation* properly speaking. But a similar influence may give rise at the same time to a general localized sensation and a vague sensation or sentiment. Thus it is that hunger is manifested by a *sensation* that we localize at the epigastrium (stomach), and also by a vague and indefinite *sentiment* that is experienced throughout the organism and which spreads to the extremities in the form of fatigue. The same is true concerning thirst, which sensation is referred to the throat and also to a general *sentiment* of languor.

The *general* non-localized *sensations* are a very interesting study for the physician; one of the most curious of these in the light of its pathological modifications is the *sentiment* of our existence; this sensation passes ordinarily unnoticed, because it is habitual and constant; it is pretty much the same as with the miller who does not notice the noise of his mill. When this sensation is noticed it indicates usually a pathological condition whose seat is most generally in the cerebro-spinal centre (hyperæsthesia), and makes us experience to a painful degree all the phenomena going on in our organism; this feeling of habitual *malaise* constitutes hypochondria.

Localized sensations are ordinarily produced under the influence of an external action on some definite portion of the surface of the body, and are conveyed to the nerve-centres by means of nerves which are always definitely determined. But should some cause act upon these nerves in any portion of their extent, we perceive the sensation which occurs, just as if the action were brought to bear upon the point where these nerves originate. If, for instance, the ulnar nerve is suddenly compressed at the posterior portion of the elbow on its inner aspect (epitrochleo-olecranon groove, or groove near the inner condyle of the humerus), we localize the painful impression so caused at the cutaneous extremity of this nerve, or, in other words, at the inside of the hand (and especially in the little finger). This phenomenon constitutes what is called the *eccentricity of the sensations;* whatever may be the point where the nerve is attacked, the sensation invariably is eccentric; even when the central portion is attacked we localize the sensation at the peripheral end of the sensitive nerve in question. Patients struck down by cerebral apoplexy complain of peripheral pains whose cause is wholly central.

These considerations afford the clew of the mechanism by which hallucinations are produced, whose cause is located in the encephalon and gives rise to certain sensations attributed by the patient to the periphery.

This explains also the associated sensations; an external sensation arriving at a nerve-centre can there produce an excitation sufficient to radiate towards the neighboring centres; these will then give us sensations identical with those we should have experienced had the excitation been produced on those nerves that make communication between these centres and the periphery. In this way a foreign body introduced into the ear may produce as an associated sensation a feeling of tickling in the back part of the throat, and perhaps even coughing and vomiting. These associations are caused on account of the nearness of the central gray nucleus of the trifacial and of the nucleus of the glosso-pharyngeal and pneumogastric, from which excitations perceived by the former radiate towards the latter.

There are examples of associated sensations still more startling that seem due to the same mechanism: in certain persons an irritation on the foot between the third and fourth toe produces a sensation of tickling in the sub-umbilical region of the abdomen; an irritation on the skin of the scrotum will give rise to pains in the right hypochondriac region, etc.

Memory and Volition. — Finally, the sensations present in addition to the preceding this peculiar fact, that they can be stored up in the cerebral organs; the impressions are fixed there to reappear at a later time; in this way are caused those phenomena designated under the name of *memory*. The sensations thus reserved in a latent condition reappear by a mechanism analogous to that of the associated sensations, and this revival of a sensation can bring on a number of others similar or analogous: as, *one idea calling up another*, and what is called *association of ideas*.[1]

[1] The cell in the spinal cord is also susceptible of preserving up to a certain point the impression which has been produced by a centripetal nerve, though generally the former retains nothing after having brought its peculiar reflex action. Thus a certain habit of reflex actions is brought about, which terminates in happening more readily and regularly. In fact, the spinal cord can be educated; we need only cite the example of persons who play upon musical instruments, who finally attain the faculty of executing a musical piece or tune almost without any conscious volition, and

However, physiology goes no farther; it has but little means of knowing what is the internal and intimate nature of the mechanism of the *seat* of *thoughts* or *ideas;* as, for example, we know that softening of the brain, characterized sometimes by gay and sometimes by sad thoughts, has its seat in the gray cortical substance; little doubt can thus be had that the seat of thought is in a general way located in this substance; as, moreover, a large number of vivisections would seem to prove.

The central phenomenon of *volition* is equally beyond our study, at least when it forms no part of association of ideas. Still, we know at least that injuries in the brain destroy those manifestations called voluntary, and paralyze the voluntary movements of the *opposite* side; viz., *movements of the right side of the body are abolished by a lesion having its seat in the left hemisphere of the brain, and vice versa.* The centrifugal conducting nerves of volition decussate on leaving the brain. However, this decussation must not be localized only at the lower extremity of the pyramids; it extends throughout a larger space from this point, to the most anterior portion of the protuberance. A lesion which may be seated in any part of this extent may then affect at the same time fibres which have already crossed (decussated) and those which have not; thus there may ensue those peculiar *alternating* paralyses, which for example may be located in the right side of the face and on the left side of the remainder of the body (see physiology of the spinal cord, pp. 43 and 45).

We find equally in the case of phenomena of motility as in the volitional phenomena associations analogous to those which we have explained in regard to sensation or sensibility. Thus a centre becoming the seat of a lively action can do so to such a degree that its activity may extend even to the neighboring centres.

This is the mechanism of all the little convulsive movements and also of involuntary associated movements. This also explains why it is that during a very intense and general muscular exertion, as for instance when lifting a heavy weight, a person involuntarily contracts the frontal muscles; as, also when sneezing, the eyes are involuntarily closed, etc.

Thus we might as a general rule state *that all our voluntary movements are associated movements*, because we cannot

without the intervention of the brain. The *cerebral memory* is simply in a higher degree a sort of *medullary memory*.

contract one muscle apart from others, but contraction of muscles usually occurs in groups; this association is wholly performed in the spinal cord by certain groupings of globules and fibres, and the brain serves only to excite this group of globules; this association is found in those movements which are purely of a reflex character, as those of defence which are observed in experiments on decapitated animals (physiology of the spinal-cord, p. 53).

Special functions of certain cerebral centres, or what is called encephalic centres.

We shall not enter into the detail of the numerous hypotheses which, even in the experimental investigations of the modern school, have founded the physiology of the encephalic organs. The system founded upon the union of specified faculties of the mind to particular circumscribed portions of the brain is regarded as an illusion (*Phrenology*, system of Gall), especially when an attempt is made to define these faculties, otherwise arbitrarily classified, according to the development of certain external portions of the skull (Craniology).

However, very recently it has been believed according to certain pathological observations that the centre of faculty of *language* or at least the *memory for words* is seated in the third convolution of the left (Broca) or right (Bouillaud) hemisphere. It is evident that perception and thought form an undefined phenomenon, which depends upon a peculiar activity of the cerebral cells and of an association of these cells connected by numerous commissures; yet our knowledge is too uncertain to localize these functions.

The tubercula quadrigemina (*corpora quadrigemina*) are the centre of visual perceptions, and of reflex movements which cause the dilatation or contraction of the iris (Herbert, Mayo, and Flourens); yet when the cerebral hemispheres are removed, luminous impressions, though perfectly perceived (the animal follows with his eyes and head the movements of a lighted taper), are not preserved and cannot give rise to an intellectual effort; in this aspect of the case the sensation must be imperfect, — the animal looks but does not see. The tubercular quadrigemina are to visual sensations what the protuberance generally is to sensations of touch, pain, etc.

It is probable that these tubercles, moreover, preside over other functions, not now known, since they appear considerably developed in animals completely deprived of the power

of sight (Talpa Asiatica, some of the Ophidio-Batrachians, Myxine); Serres also considered these as centres for co-ordination of movements; the explanation of this seems to be in the fact that these tubercles have some relation to *excito-motory impulsions*, which would authorize their classification with the cerebral centres, as a medium between the protuberance and the clusters of cerebral and cerebellar cells (see p. 33, fig. 12).

The functions of the cerebellum are a problem difficult of solution; experimentation and observation from pathological conditions give us but negative and contradictory results; ablation of the cerebellum shows that this large portion of the encephalon takes no part in the intellectual functions, strictly speaking, nor in the manifestations of sensation, memory, instinct, or volition. Its peculiar functions are so difficult to define that almost all possible opinions have been proposed. Leaving out of consideration the opinion of Willis, who, at the time when the theory of the *animal spirits* held sway, made it the point of departure for the innervation of *organic functions*, we notice that some physiologists (Lapeyronie, Pourfour du Petit, Dugès), basing their opinion upon the apparent continuity of the inferior cerebellar peduncles with the posterior columns of the spinal cord (conductors of sensation or sensibility), considered the cerebellum as the central organ of *sensibility*, the *sensorium commune* to which all the peripheral sensations pass for elaboration and arrangement, especially including the auditory (Foville) and visual sensations (Lussana). We have already noticed that this *rôle* of the centre of sensation belongs in part to the protuberance and in part to the tubercula quadrigemina. With less reason, but perhaps more fortunate in his hypothesis, Gall considered the cerebellum as a centre of *animal love*, or *erotic passion;* indeed, in spite of the experiments and contradictory observations by Leuret, Ségalas, Combette, and Vulpian, we notice several reasons brought out by experimentation and clinical observation by Budge, Valentin, Wagner, Lussana, which would seem to give some appearance of reality to the hypothesis of Gall, and to assign an important function to the middle lobe in the manifestations of genital instinct.

The cerebellum, however, seems to have an important part in the apparatus for the co-ordination of movements as appears from the experiments of Rolando, and especially from the more recent and numerous experiments of Flourens; in the

animals (birds) from which this latter physiologist removed the cerebellum, "flying sensations and perceptions remained; the possibility of executing combined movements likewise persisted, but the co-ordination of movements into movements of regulated and definite locomotion was lost." This has been the view adopted by the majority of physiologists; and Lussana has even gone further, and attributes to the cerebellum the function of the centre of *muscular sensibility.* However, these functions of locomotion are manifested only when the deeper portions of the cerebellum are injured, whilst superficial injuries do not give any result, and leave us without any indications of the functions of the cortical layers of the cerebellum. Moreover Vulpian and Philippeaux have caused no disturbance of locomotion in fishes after ablation of the cerebellum; let us recall to mind also that physiology of the spinal cord has furnished almost all the elements necessary to explain the reflex mechanism of locomotion; moreover, Küss saw a rabbit whose head he had amputated with dull scissors, thereby hacking the head so as to prevent hemorrhage, jump from the table and run the whole length of the room with a perfectly defined movement of locomotion, and we shall arrive at the conclusion that, in spite of the very numerous solutions that have been offered to explain the physiology of the cerebellum, we still possess no precise notion of the functions of this nervous centre.

The *corpora striata* and *optic thalami* are inexcitable, as well as the gray axis of the spinal cord, and all the gray centres; we cannot then arrive at a knowledge of their functions except by their destruction in animals, or by the study of the clinical phenomena which follow their alteration, either by the presence of a tumor or by a hemorrhage. In these cases no lesions of general sensibility have been proved, nor of any special sensibility, and we must admit that the *optic thalami*, in spite of their name, have no more concern with *vision* than the *corpora striata* have with the sense of olfaction. Lesions of these centres produce only paralyses (paralysis on the opposite side, as we have seen *à propos* to the conductors in the spinal cord), and we may consider the corpora striata and optic thalami as grand *excito-motory* centres, but without assigning to the former the movements of the posterior extremities, and to the latter those of the anterior extremities.

The *corpus callosum* (trabs cerebri), and the different commissures between the cerebral hemispheres taught in anatomy,

are by no means the *seat of the soul*, as held by certain authorities; these are only bridges of white substance that harmonize the functions of the two hemispheres which they connect; but here, moreover, we must not attach a meaning to words nor pretend to a decision not supported by the facts; as, for instance, is done by Treviranus, who asserts that the corpus callosum furnishes the brain with the faculty of *comparisons*, as if comparison were made between the thoughts which come from the left and right, and not between impressions, or successive thoughts (Dugès).

The *cerebral hemispheres*, and especially their gray cortical substance, are the most essential portion of the brain. Here are accomplished the elaborations of the *sensations* in the form of *thoughts*. The experiments of Flourens, from which Longet especially has drawn legitimate conclusions, prove that animals from which the hemispheres have been removed, as we have before remarked in connection with the protuberance and tubercula quadrigemina, continue to feel, hear, see, and receive the impressions of taste; but that these impressions do not remain nor awake any response, nor seem to produce any associations of ideas; they do not *look* nor *hear*, nor *smell*, nor *taste;* in short, the cerebral lobes "are the receptacle where all sensations take a distinct form, and produce a continued remembrance." There may be a perfect sensation without the cerebral lobes; but this sensation bears a resemblance to that effect which is noticed in a person wrapt in profound meditation, and receiving an external irritation (as, for instance, when a fly lights upon the hand), but whose meditation is not in any way interrupted, and who does not appear to notice the irritation (Vulpian, Taine).

On the other hand, the cerebral lobes preside over *spontaneous movements*. An attentive analysis of the movements of a frog or of a fish deprived of the cerebral lobes proves that these creatures swim only under the influence of reflex actions perfectly co-ordinated, which the impression of the water in contact with their integument may provoke; they progress as if impelled by a pre-established mechanism, as if subjected to a reaction which makes their progress an imperious necessity, until a new impression, as for instance coming in contact with the borders of the vessel or basin, causes the frog to assume a state of immobility and normal posture, a necessity no less imperious than the first. There are not seen in the behavior of the animal any of those capricious changes, or spontaneous movements from repose to activity

and *vice versâ*, that characterize animals with uninjured cerebral lobes, and who hence are capable of *volition* or *intentional spontaneity*.

The faculties called intelligence and instinct unite these opposing phenomena, *perception* and *thought* on the one hand, *volition* and *spontaneous movements* on the other. The seat of the phenomena which we have just analyzed is localized in the cerebral hemispheres, especially in the gray cortical substance of these hemispheres. An animal deprived of these hemispheres is plunged in a peculiar sleep, dreamless sleep (Flourens). On the contrary, pathological conditions which over-excite the cerebral convolutions awaken in them chains of disordered thoughts, which a diseased brain considers external realities; of this order are the delirium in meningitis, madness in its acute and chronic varieties; thus those who are concerned in the care and study of insanity seek to attach to these organs the alterations of intelligence, especially the *somatic element*, in which *psychical disturbances* are simply the manifestation of the disease.

The development of the cerebral convolutions, and, perhaps we might even say, the *quality* of the gray cortical substance, are in proportion to the amount of intelligence possessed by the animal; idiots seem to have fewer nerve globules than persons of sound intellect. In the autopsy of idiots portions of the brain are found made up of connective tissue, and containing a large amount of embryonic globules which have not been transformed into nerve elements.[1]

D. Great Sympathetic.

The great sympathetic is composed of a series of *ganglions* arranged along the side of the vertebral column (Fig. 15), at the side of each vertebra (except in the cervical region, where there are groups of three great ganglions). The ganglions of the same side are connected by commissures, whence result cords arranged in chaplets.

Moreover, these *globular groups* send commissures from one portion towards the spinal cord (*rami communicantes*), and from another portion towards the viscera and other organs in general (*nerves of the great sympathetic*). At a certain distance from the chain of the great sympathetic, in the course of those commissures, going either towards the

[1] Küss *in* P. Ad. Rousseau. Thèse de Strasbourg, 1866. (Note "Sur le Rôle et l'Importance du Globule en Physiologie.)

spinal cord or the viscera, new ganglionic masses are found. Of this class numerous globular clusters are arranged like the rounds of a ladder on the nerves that return to the viscera. The most remarkable of these groups are the *semilunar*

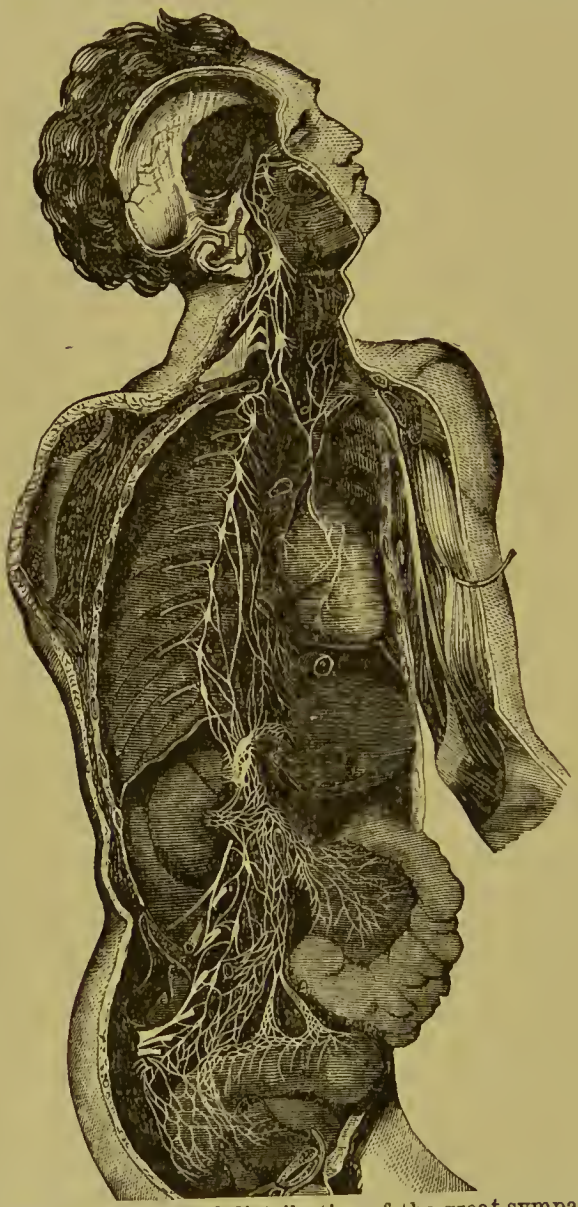


Fig. 15. — Direction and general distribution of the great sympathetic nerve. (Dalton, "Human Physiology.")

ganglion, called by Bichat the *abdominal brain*. Finally, at a more distant portion in the path of the visceral nerves a new series of ganglions are distributed in the walls of the organs, being ordinarily only of microscopical dimensions.

Some of these occur in the tissue of the intestinal walls, in the muscular structure of the heart, in the bronchi, etc. (visceral or parenchymatous ganglions).

By means of these numerous ganglions or clusters of nerve globules, the sympathetic system seems to serve as a centre of certain reflex actions, as it possesses fibres having centrifugal, and others having centripetal, properties. The great sympathetic has been considered the seat of all those nerve phenomena more or less mysterious that have been embellished with the name of sympathetic, and which we now call reflex phenomena. It must, however, be remembered that the great sympathetic is in no wise a system by itself; it simply shares in the properties and functions of the medullary system, and is associated with the latter.

In fact, its nerve fibres and filaments are excitable to the same agents as the spinal nerves, that is, to electricity and chemical agents; but the physiological excitant that we have previously designated by the name of *volition* or *will* has no effect upon this system; consequently, the movements which are produced in the department of the great sympathetic are all involuntary. On the other hand, those movements resulting from the artificial excitation of the nerve require a definite amount of time for their production. They are manifested slowly and cease slowly. This new difference has the same relation to the peculiar nature of the nervous and sympathetic fibres as in the case of the fibres of Remak (pp. 25 and 26), and of the muscles to which they are distributed (*smooth muscles;* see farther on). The excitation of the filaments of the great sympathetic gives also origin to the phenomena of sensibility, but an intense as well as long-continued irritation must be brought to bear upon them. In the pathological conditions the great sympathetic is much more excitable, and becomes both the seat and conductor of a large number of painful sensations. Formerly, too, the independence of this nervous system in its relations to the cerebro-spinal system was much exaggerated. It was made to preside as a central organ over the functions of the viscera in general, and more especially of those belonging to nutrition. Experiments by Cl. Bernard demonstrate that the sub-maxillary ganglion may serve as a centre for the salivary secretion; yet this result has lately been denied by Schiff.[1]

[1] Mau. Schiff, "Leçons sur la Physiologie de la Digestion," Vol. I., 12th Leçon.

The ganglions that occur in the wall of the viscera at the terminal branches of roots from the great sympathetic serve as a centre for partial movements of the visceral muscles, and regulate, by way of illustration, the peristaltic contractions of the intestinal walls. Other ganglions (of Wrisberg, semi-lunar, of the hypogastric plexus, etc.) might be considered as provisionary centres where the nervous action coming from a higher point can be accumulated. The majority of the phenomena of the visceral functions have as their nervous centre the spinal cord, and even in the *vaso-motor* functions (see circulation) the sympathetic has only a power of impression derived from the superior portion of the spinal axis. The same may be said in reference to its influence on the heart, and most of the visceral reflex actions whose centre is found in the spinal cord; so that the expression "great sympathetic system" has at this present time but little physiological signification.

PART THIRD.

CONTRACTILE ELEMENTS.—MUSCLE AND ITS ADJUNCTS.

I. Muscles in General.

The muscular elements are produced by metamorphosis of the globules of the embryo. By studying their formation we may best understand the *three types* presented by the muscular system,—the *contractile cell*, *smooth fibre*, and *striated fibre*. We notice, at the same time, that the property of changing their shape (or *contractility*), which is characteristic of these different kinds of muscles, is only the same property, carried to a higher degree, which we have ascertained belongs to globules in general.

When an embryonic globule is slightly lengthened, and its nucleus becomes more visible, etc., we have the *contractile cell* (Fig. 16, 1), as it is found, for instance, in the smaller arteries.

When the cells are united at the ends in such a way as to form a varicose fibre, with elongated nuclei in different parts, and granular contents, we have the *smooth fibre*, in which, moreover, are found all the elements of the cell (Fig. 16, 2).

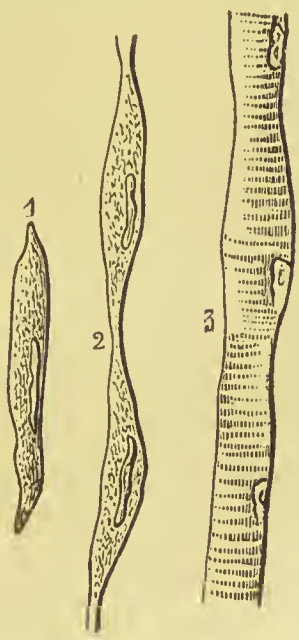


Fig 16.—Diagram of the three forms of the contractile or muscular element *

Finally, as the fibre straightens, and the fusion of the cells becomes complete, we have the *striated fibre* (Fig. 16, 3), the

* 1, Contractile cell. 2, Smooth muscle. 3, Striped muscle.

envelopes of the primitive cells being represented by the covering of the fibre, or sarcolemma; the cellular nuclei by corpuscles, placed at intervals upon the inner surface of this covering; and the cellular contents by the granular contents of the fibre: the latter appear to be formed from a liquid portion, and from granulations (*sarcous elements* of W. Bowman) which, being grouped in series, either perpendicular, or parallel with the axis of the fibre, give us muscles with longitudinal or transverse striæ, the latter form being the most common (Fig. 17, *a* and *b*). It is not unlikely that other effects are due to the artificial mode of preparation.

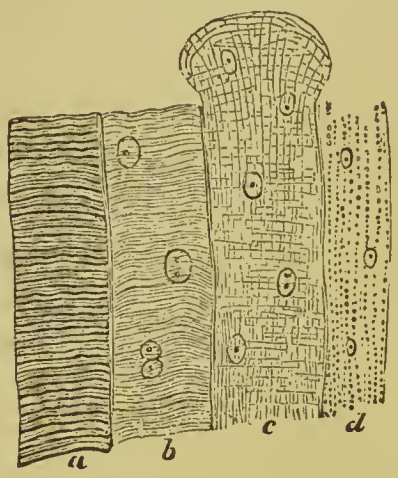


Fig. 17.—Different appearances of the striped muscle.*

The *striated muscle* has been the most minutely examined, and we will, therefore, begin our study of the muscles with this form.

II. Striated Muscle.

These muscles appear as clusters of fibres, remarkable on account of their *transverse striation*. Histological analysis shows this fibre not to be the simple element which it appears; it is itself composed of *longitudinal fibrils*, exhibiting small nodosities arranged in clusters, one above the other; the regular arrangement of the nodosities of the adjacent fibrils in transverse series produces the striated aspect of the fibre as a whole. (See Fig. 17, *a*, *b*, *c*, *d*). Opinions differ as to the nature of these nodosities. According to Ch. Robin, they are caused simply by the appearance of points which are alternately light and dark, and are themselves caused by a difference in refraction in the different parts of the fibril; while Ronget supposes them to be produced by the spiral twisting of the fibrillary filament, forming a helix, the coils of which are more or less closely brought together accord-

* *a*, Normal appearance of a recent primitive fasciculus, with its transverse striæ. *b*, Fasciculus treated by dilute acetic acid (the nuclei showing more distinctly the nucleoli). *c*, Under the action of concentrated acetic acid the contents escape at the extremity of the envelope (sarcolemma). *d*, Fatty atrophy. (Virchow, "Pathologie Cellulaire.")

ing to the condition of the muscle. We shall consider this explanation again when analyzing the ultimate action that constitutes what is called the *contraction* of the muscle.

The principal feature in the study of the muscle is that it changes its shape, and appears under two different forms; thus a fusiform muscle, meeting with no opposition, becomes globular under certain circumstances. The former condition is usually called the *state of repose*, and the latter the *state of action*. In order not to anticipate, we will call the first simply form No. 1; the second, form No. 2 (Fig. 18).

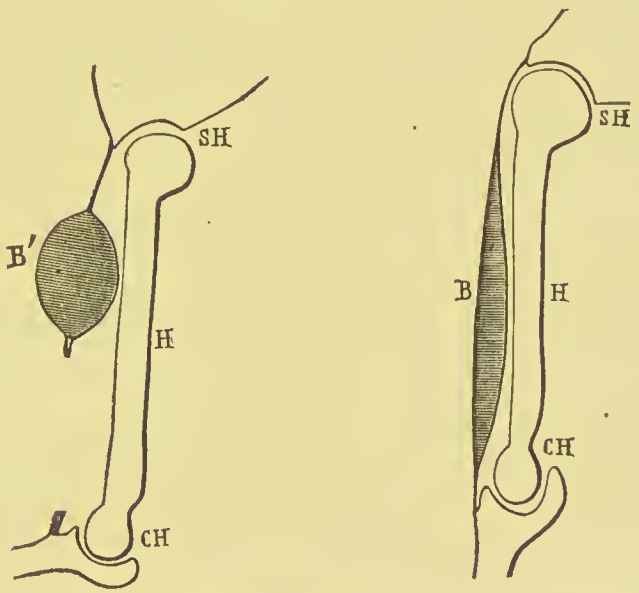


Fig. 18.—The muscle, under forms No. 1 and No. 2.*

We will, then, proceed to examine the properties and phenomena exhibited by the muscle under form No. 1; and, afterwards, those under form No. 2. As the muscle originates from the globules, and still represents, in its structure, the elements of which they are chiefly composed, we shall find both in it, and in the two forms which it takes, the principal physiological properties of the globule; viz., elasticity, chemical phenomena, electro-motor power, etc.

These properties being known, we shall speak more at large of those which are chiefly made use of in the animal

* SH, Articulation of the shoulder joint. CH, Articulation of the elbow. H, Humerus. B, Biceps in the state of repose (form No. 1). B′, Biceps assuming the form No. 2, in consequence of section of its tendon. (The tendon of the biceps is actually inserted into the radius, but since, during flexion, the latter becomes a fixed body with the *ulnar*, the fore-arm is represented in the diagram by a latter bone, in which the biceps appears to be inserted.)

economy, especially the faculty of passing from the first to the second form; and, in seeking for the reason of this phenomenon, we shall study, in the muscle, as we have already done in regard to the cells in general, that most essential property of all living elements, *excitability* or *irritability*.

A. The Muscle, under Form No. 1.

Elasticity. — One of the most remarkable properties of the muscle is its *elasticity*.[1]

By *elasticity* we mean that property of bodies by which they are diverted from their primitive form, and return to it as soon as the extending cause ceases to act. Different bodies present great differences in this respect, and the elastic properties vary, according to whether the change is made with more or less facility, and the return to the original form is more or less complete. We say that the *elasticity* is *perfect* when this return is perfect (an ivory ball, for instance); that *it is imperfect* when the return is not complete (example, a lump of dough); that the *elasticity* is *great* when the change is made with difficulty, and the return is sudden (as with a steel blade), and that it is *slight* when the change is easy, and there is slight tendency to return to the original form (example, a willow twig).

The muscle, under form No. 1, may be said to be *slightly* and *perfectly* elastic. In this example muscles are flabby, and may be easily stretched, so that the arm, deprived of its muscular envelope (directly after death), is no more readily moved than when the muscles were in place; this proves that in this state the muscles readily distend (*slight elasticity*), and afterwards assume their *original condition* (*perfect elasticity*). In the same way, the muscular bags (auricles, ventricles, stomach) are so easily distended by any thing which has a tendency to dilate their cavities, that their elasticity can be compared only to that of a soap-bubble.

This *slight* and *perfect* elasticity is not a *purely physical* property of the muscle; for it depends on the life and nutrition, or at least on the chemical composition, of the muscle, and this composition is directly under the influence of the life of this element (circulation and innervation). When the muscles have remained long in a state of inactivity, and are, consequently, ill-nourished, they lose a portion of their

[1] See Ritter. "Des Propriétés Physiques du Muscle." Thèse de concours. Strasbourg, 1863.

elasticity, — witness the pain and difficulty experienced in extending the forearm, after it has been long kept in a sling.

The muscles of a corpse are at first flabby and extensible, preserving any shape which may be given them; still they are slightly, but *imperfectly*, elastic; later, they enter the state known as that of *cadaveric* (*corpse-like*) *rigidity*, when immense force is required to stretch them out, and, being once stretched, they can no longer regain their original form, and thus become *strongly* and *imperfectly elastic*. This cadaveric rigidity was formerly attributed to coagulation of the fibrin of the blood (J. Müller); but it is now generally supposed to be owing to the coagulation of the *myosin*, or of its derivative, the *syntonin* (Kühne), an albuminoid substance, which coagulates spontaneously, and closely resembles the fibrin of the blood. The muscular fluid coagulates by heat; thus the cadaveric rigidity of a muscle may be produced instantaneously, by immersing it in a fluid at a temperature of 45° c. (See farther on, p. 82.)

We see, thus, that *slight* and *perfect elasticity* is, up to a certain point, characteristic of the life of the muscle; and that it differs entirely, in this respect, from the elasticity of the ligaments, of the bones, and, above all, of the elastic tissue; since their elasticity remaining always the same, depends only on the mechanical arrangement of the fibres of which these tissues are composed, and is thus purely physical. This cannot be said of the elasticity of the muscle; neither can we look upon it as an essentially vital property, for it appears to depend principally upon the chemical composition of the muscle. In fact, by injecting hot water (experiment of Brown-Séquard), or defibrinated blood, or serum, or even any simple alkaline liquid, into the arteries of an animal lately killed, it may be for a time preserved from this rigidity, which is brought on by the acidity of the muscle, and is opposed by its alkalinity. If, for instance, the arm being in repose, and the tendon of the biceps cut, we find that it immediately shrinks a little; and, having been previously slightly extended, assumes its natural form only by the natural distance of its points of insertion, and, consequently, exerts upon these latter only slight traction. This is called the *tonicity* of the muscles; but we see that it is not a special property of the muscle, but is only the result of its elasticity, brought into play by its insertions, the distance of which prevents it from perfectly assuming its proper form;

tonicity is only its tendency to assume that form. Neither is the so-called tonicity of the sphincters an independent property of their elasticity. These muscles, under their natural form, No. 1, are arranged in order to completely close the openings which they circumscribe, so that these openings really do not exist, and are only formed when dilated by a body animated by a certain force, which brings into play the *elasticity of the sphincters* (tonicity of authors). This *tonicity* or *perfect elasticity of living muscle* is under the dependence of the nervous system. When the nerves that belong to these muscles are cut, the tonicity disappears, the muscles become flaccid, and the sphincters are relaxed.[1] The origin of tonicity is not yet demonstrated. It has a reflex character. Brondgeest has shown that if the sensory nerves, coming from a part where the muscles are in a perfect condition of *tonicity*, be cut, this tonicity will immediately disappear (*vide* p. 108).

These considerations concerning the elasticity and the *natural form*, No. 1, of the muscle, help us to solve a question which is differently answered by other writers: *Are the flexors of the extremities superior in force to the extensors, or vice versa?* From the fact that in repose, or after death, the limbs are generally found to be in a state of semi-flexion, it has been supposed that there is a predominance of force on the part of the flexors; but where there is repose there is no struggle, and without a struggle there can be no predominance of force. This position only proves that the flexors are shorter than the extensors, and that extension, under these conditions, brings into play the elasticity of the flexors. But suppose the state of repose to cease, and the struggle begin, as, for instance, in tetanus, when all the muscles are contracted, and we shall find all the extremities, and the trunk itself, extended; whence we conclude, contrary to the majority of writers, *that the extensors are more powerful than their antagonists.*

Chemical Phenomena.—The muscle, in its natural form, No. 1, lives and receives nourishment, that is to say, its chemical composition is constantly changing: it also breathes; a muscle, even though detached from the body, as long as it lives continues to absorb oxygen, and give out carbonic acid; and the longer it can breathe, the longer it lives, as, for instance, when

[1] See Cl. Bernard. "Propriétés des Tissus Vivants." When the nerve of a muscle is cut, the venous blood which flows from the muscle closely resembles arterial blood.

placed in an atmosphere containing oxygen.[1] In the living animal, the venous blood which flows from the muscle differs essentially from the arterial blood which enters it, having less oxygen, and more carbonic acid.

The respiration of a muscle is in direct proportion to its life, and as the latter depends in a great measure on the trophic (nutrient) influence of the nervous centres, if the nerve of a muscle be cut, the gaseous exchange will be considerably less, as well as the elasticity be diminished (see preceding page). We explained the simultaneous modification in the chemical phenomena and the elasticity of the muscle, by saying that its respiration is accelerated by its *tonicity;* the meaning of which word we have already given.

It should be added that the muscle, under form No. 1, is alkaline; under this form, no doubt, its chemical phenomena, are not sufficient to produce acids capable of neutralizing the alkalinity of the blood contained in the muscle.

Electro-motor Power.—The muscle possesses electro-motor properties, that is to say, it gives rise to electric currents; this may be proved by making the two wires of a galvanometer communicate, one with the interior part of a muscle, or transverse section, the other with the outside of the same muscle, or longitudinal section; the current flows always from the surface to the centre; that is, the surface, or longitudinal section, is positive in relation to the centre, or transverse section (Fig. 19).

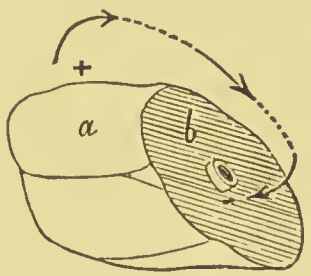


Fig. 19.
Muscular current.*

Presuming that this electro-motor power might furnish the key to the principal properties of the muscle, especially to that by which it passes from form No. 1 to that of No. 2 (for we

[1] Hermann (Berlin, 1867) maintains that the phenomena of gaseous exchange presented by the muscles, when separated from the body, and brought into contact with the air, are phenomena of *simple putrefaction.* But Paul Bert has shown them to be really phenomena of respiration, of life, and has proved the existence of these respiratory exchanges, though in a less degree, in different tissues. See "Leçons sur la Physiologie comparée de la Respiration." 1870., 4e Leçon;—"*Respiration des Tissus.*"

* In the galvanoscopic circuit the current flows from *a* to *b*, as indicated by the arrows. *a*, Longitudinal surface of the muscle, positive (+). *b*, Section or transverse surface negative (—).

find that, in this case, the current is reversed or disappears) much study has been given to this subject; and, after specifying the conditions of the current, it has been sought to explain them by what is called the theory of *peripolar-electric molecules*. We will not, however, explain in detail this theory, for it is probable that the study of these currents is not of supreme importance in the physiology of the muscle, but that they should be considered simply as the result of the chemical phenomena of which the muscles are the seat, and which are more or less active as the layers may be more or less superficial. In fact, the shape of the pieces of muscle employed in experiments has great effect upon the direction of the current; a muscle may possess its normal electric current, and yet have lost all its other properties; thus, poisons which kill the muscle have not always the same effect upon its electro-motor power; finally, similar currents have been observed in living tissue of various kinds, even in vegetables, as, for instance, in pieces of the pulp of a potato.

B. *The muscle, under form No. 2.*

The muscle, in this state, only differs essentially in a change of form from what it was in the preceding state: it is shorter and thicker; a fusiform muscle becomes globular. The difference may, in general, be estimated at $\frac{5}{6}$, that is, the muscle under form No. 2, becomes shorter by $\frac{5}{6}$ of its former length under form No. 1. But its transverse dimensions increase in exact proportion to the diminution of its longitudinal dimensions, and there is, consequently, no change in its bulk. If we place in a graduated vessel, full of water, a muscle of form No. 1, and by any excitation cause it to pass into form No. 2, we shall find no change in the level of the fluid. Lately, however, Valentin has ascertained, by an extremely minute process, that a muscle, in passing from the first to the second form, increases in density in the ratio of $\frac{1}{1300}$, but this fraction represents such a slight diminution of bulk that it seems quite unworthy of notice.

The bulk remaining the same, we have then, in order to make a comparative study of the muscles, under form No. 2, only to consider it in the triple aspect of the properties already studied in form No. 1: its elasticity, chemical phenomena, and electro-motor power.

Elasticity. — The muscle in form No. 2, when not prevented from completely taking this form, is as soft and elastic as in form No. 1. If it is then handled, it is found to be ex-

tremely soft. This is a phenomenon occasionally observed by surgeons in an amputated limb, especially the thigh; the muscles which have been cut are seized with tetanus, contract, and pass into form No. 2. Nothing hinders their taking this form completely, as they have no longer any lower insertions, and they withdraw towards the root of the limb, and here form a soft, fluctuating, and globular mass, which has been compared to a collection of liquid. It even appears, and it is true, that the muscle is softer under form No. 2 than under form No. 1. If we attempt to reduce the muscle from the second form, we find that it allows itself to be extended easily, and, after having been drawn out, returns perfectly to the shape from which it was diverted, and is thus, exactly as in form No. 1, *slightly* and *perfectly* elastic. Besides being softer, it is more slightly elastic under form No. 2, that is, it is more easily diverted from this form than from form No. 1: this is shown by two of Weber's experiments.

1. This physiologist constructed, out of muscular fibres, twisting pendulums, and, on setting the needle in motion, observed that the oscillations which occurred are more rapid when the muscle is under form No. 1 than under form No. 2; in other words, in experimenting on form No. 2 a slackening was observed, which indicates a less degree of elasticity and cohesion, the rapidity of the twirling of the needle being always in proportion to the elastic force of the twisted thread.

2. By a second experiment Weber ascertained that a weight suspended to a muscle under form No. 2 stretched it more than when it was attached to that of another under form No. 1. We can easily understand that the greater the weight the greater the elongation, and that, by constantly adding to the weight, we at length give the muscle under form No. 2 a length equal to that which it would have under form No. 1, even equal to its length under this form, if stretched out by the same weight; and, finally, even to a greater length than if stretched out by the same weight under form No. 1. On arriving at the weight which yields this last result, we notice an apparently paradoxical phenomenon, which is, that by loading with this weight a muscle under form No. 1, and then making it pass by some excitation into form No. 2, we find that, instead of shortening under the influence of the weight, on the contrary it lengthens, which is simply the result of the muscle under form

No. 2 being more slightly elastic, or less resisting, than under form No. 1. This singular phenomenon of *a muscle which lengthens while contracting* proves, that what is called *the active state* (form No. 2) has nothing to do with the shrinking, and justifies the selection that we have made in using the expressions, *muscle under form No.* 1 *and No.* 2, in preference to speaking of *contracted* or *retracted muscles.*

Thus, in form No. 2 the elasticity of the muscle is *slight* and *perfect*, less even than under form No. 1.

These propositions appear in singular contradiction to what is commonly observed in that condition which we call a *contracted muscle*, that is, one which has passed, or rather, *is passing*, into form No. 2. Any one may prove for himself that the biceps, for instance, when contracted is exceedingly hard, and appears to be strongly elastic, that is, offering great resistance when drawn out, so that we can hardly believe in the softness of the muscle under the second form. This is because, on account of their arrangement with regard to the skeleton, the muscles in the living body hardly ever attain the second form any more than the first (see above, *tonicity*). When, for instance, the biceps passes into the second form, it has a tendency to *grow shorter by five-sixths of its length;* but the displacement which it may cause to the bones allows it to shorten, at the most, by only one-sixth or two-sixths; we have then a muscle of the second form, forcibly drawn out, exactly like a strip of india-rubber stretched violently; it is necessarily, then, extremely hard and resisting to the touch. This hardness is not caused by the muscle being in the second form, but by this form being forced, and not perfectly attained; it does not arise from the contraction of the muscle, but from the tension that it undergoes during its contraction. This hardness is to the second form what the so-called tonicity was, in a less degree, to the first form.

In order that a muscle may take the second form perfectly, the bones must be disarticulated, or the muscle must be cut at one of its insertions, after which it will be seen to shorten considerably, at the same time growing broader (see Fig. 18, p. 69). We have mentioned this already, when speaking of the form of the muscles of the thigh, which are in a state of tetanus after amputation. Being then subjected to traction, the muscle hardens, and as the forcible elongation increases the resistance becomes greater, exactly as with a strip of india-rubber. Let this elongation be caused by the relation

of the muscle to the resisting skeleton, and in the case of the hardening of the biceps, which we took for an example, we shall find that it is not a feature of the second form, but of the elongation which the muscle undergoes, and thus prevents it from assuming that form.

These considerations show that the name of *active muscle*, applied to the muscle in the second form, is extremely improper. The muscle is no more active under this form than under the first, when this form is easily assumed; and when, moreover, if the muscle meets with resistance, it might then be said to be *passive*, like a strip of india-rubber, which cannot be said to be active because it shows a tendency to return to that form from which it was diverted by being stretched. The only activity of the muscle consists in its passage from the first to the second form; but in each of these forms it is passive, because its insertions constrain it as much in the former as in the latter case.

Chemical Phenomena. — We have seen that the muscle, under the first form, absorbs oxygen, and gives off carbonic acid; that it is, in short, the seat of combustion, the materials for which are furnished by the blood. The same is true of the second form, with the exception that, in this case, *the combustion is much more active;* thus, on analyzing the products evolved by a muscle which has been made to pass into the second form, or on examining the waste of any entire organism during severe muscular labor, we find a greater absorption of oxygen and evolution of carbonic acid. Combustion then appears to be sufficiently active for the formation of acids, so that in a muscle which is fatigued, that is, which remains long in the second form, the muscular fluid becomes less and less alkaline, and at length completely acid: the acid thus formed is called sarcolactic acid.

The combustion which takes place in the muscle is shown immediately by the aspect of the blood which flows from it, and which resembles venous blood, *black blood* (rich in CO^2 and poor in O), the resemblance being greater in proportion to the energy of the muscle. Thus, when all muscular contraction ceases, as in syncope, the venosity of the blood diminishes to such a degree that the blood which flows from an incision made in a vein shows nearly all the distinguishing features of arterial blood.[1]

[1] Brown-Séquard, "Du Sang rouge et du Sang noir," 1858. Cl. Bernard, "Liquide de l'Organisme," 1859.

The materials of this active combustion are principally hydrocarbons, that is, the fatty and amyloid substances produced in the blood; in other words, the aliments called respiratory, for the muscle oxidizes scarcely any nitrogenous substances, and muscular labor causes scarcely any increase in the excretion of the urea.[1]

[1] The fact that the muscle, when at work, consumes principally hydrocarbon aliments, and not albuminoid substances, is quite a recent acquisition to science, and is a part of the knowledge lately obtained as to *the mechanical equivalent of heat*.

Liebig had divided all aliments into *respiratory* and *plastic*. The former, by their combustion, produced animal heat; these were the fatty substances and sugars, hydrocarbons, in short: the latter, represented by the albuminoids, were intended to repair the tissues, especially the muscles. As to muscular labor, it was produced by the muscle at the cost of its own substance, the albuminoid aliments thus alone supplying the material for it.

The new ideas as to mechanical labor, and its relations to heat, derived from the researches of Rumford, of Tyndall, of Joule (Manchester), of Mayer (Bonn), and Hirn (Logelbach), showed that heat and mechanical labor are the same thing, or, at least, are two equivalent forces;* that one is transformed into the other, according to the law of *the equivalence and constancy of forces*, and that, for instance, a *calorie* may be made to produce 425 kilogrammètres; that is to say, that the great heat which raises one kilogramme of water one degree can also, under another form (labor), raise a weight of one kilogramme to the height of 425 metres: thus the number 425 expresses the *mechanical equivalent of heat*.

Now the muscle is also a machine; it transforms heat into mechanical labor (see the text, some lines farther on), only it is a more perfect machine than any manufactured one, a machine which, with a much smaller weight, transforms into labor a far larger part of the heat produced (one-fifth in place of one-tenth, as given by the best steam engines).

If, then, we consider muscular labor as transformed heat, its source must lie in the combustions which produce heat, and the muscle must be looked upon, not as an apparatus which consumes its own substance, but as one which serves as a place of combustion for the materials which produce heat or labor. This was the hypothesis put forth by Mayer, in 1845, when, relying on the principle of the constancy of forces, he first looked upon heat and muscular labor as manifestations of living forces, and considered them as emanating from one and the same origin, combustion.

From that time the division, as made by Liebig, of aliments

* See Paul Bert: Article "Chaleur," in the "Nouveau Dictionnaire de Médecine et de Chirurgie Pratiques," Vol. VI.

We see, thus, that muscular contraction (or the passage of the muscle from the first to the second form) must be reckoned first among the sources of animal heat, on account of the active combustion which is then produced. If, indeed, a

into respiratory and plastic, attributing to the latter (albuminoids) the source of muscular labor, could only be admitted after direct proof. Reasoning first led to the belief that muscular labor, being a form of heat, must derive its origin from aliments whose combustion furnishes the greatest degree of heat, as the fats and hydrocarbons. And Mayer calculated that if it was true that the muscle consumes either its own substance or albuminoids (which comes to the same thing), the heat developed by the oxidation of these substances is so trifling that a man would have entirely consumed his muscular mass after a few days' labor.

The question could only be decided by direct experiment, and the proof needed was very simple. We shall see farther on that the residuum of combustion of the albuminoids is essentially constituted by the urea eliminated by the kidneys; if, during mechanical labor, a large amount of albuminoids are consumed, there will be a great increase of urea in the urine.

After some unsatisfactory experiments by Lehmann and Speck, and some, more conclusive, by Bischoff and Vogt, Fick and Wislicenus solved the problem in a remarkable manner. These two physiologists ascended, fasting, one of the high mountains of the Bernese Alps, measuring carefully the quantity of urea eliminated by the kidneys during and after the ascent. In the case of one of them the labor developed by this ascent may be represented by 181 287 kilogrammètres, yet no increase in the urea was observed either during or after this very severe muscular exercise. We see thus that the muscle, as the source of labor or heat, consumes only hydrocarbons and fats, and not albuminoids.

To this satisfactory experiment may be added some considerations of comparative physiology. The herbivorous animals, that is, those which feed principally on hydrocarbons, are capable of developing a much greater degree of force than the carnivora, which are nourished by albuminoids; thus man for mechanical labor makes use only of the herbivorous animals (the horse, the ox). The granivorous birds are in general more active, and develop more heat and labor, than the carnivorous. This fact is still more striking in the case of insects: thus, among the acari some live as parasites on animals, while others feed on flour or sugar (for instance, Glyciphagi); the former being remarkable for the slowness, and the latter for the almost incredible rapidity of their movements. An experiment of this kind, in regard to food, has also been made upon man. An Englishman, Harting, found, after submitting to a regimen of fifteen hundred grammes of meat a day, with scarcely any hydrocarbons, that he was reduced to an extreme degree of muscular weakness.

muscle in which contraction occurs passes perfectly into the second form without meeting with any obstacle, it gives rise to heat only; but if, as in the normal condition, it cannot perfectly attain this form, on account of the resistance which it has to overcome, we find that, on hardening, it evolves only a part of the heat produced by the combustion of which it is the seat, the rest being transformed into mechanical labor (Béclard).

Electro-motor Power. — We have seen that under the first form the muscle possesses an electro-motor power, by means of which its surface is positive, in relation to its interior.

If the wires of a galvanometer are placed in contact with a muscle under the first form, one with its surface or longitudinal section, the other with its transverse section; so as to ascertain the current, which in this case is directed from the former surface to the latter in the galvanometrical circuit, and the muscle is then made to pass into the second form; we find that the needle, which the current at first caused to swerve, returns to zero, and oscillates on this side and above it (Du Bois-Reymond). Thus the electro-motor condition of the muscle is changed: this is what is called *negative variation* of the current of a contracted muscle. But, as we have seen that no conclusion can be drawn from the electro-motor power of the muscle under its first form, so nothing positive can be affirmed as to its *negative variation* in the second form, for it is still impossible to say whether the latter is due to the suppression of the primitive current, to its simple diminution, or even to its being replaced by a contrary current.

Du Bois-Reymond, who discovered *negative variation*, considered this phenomenon as the result of the *weakening* of the normal current (electro-motor) of the muscle when in the state of repose, which weakening would allow of the manifestation of a contrary current, due only to the secondary polarities of the wire of the galvanometres (polarization of the electrodes. — See Wundt's "Physique"). Matteucci believed, on the contrary, in a *complete inversion* of the normal current of repose. Experience has shown that Du Bois-Reymond was right, for, by constructing electrodes which undergo no polarization (amalgamated zinc, dipped in a solution of sulphate of zinc, Regnault), it has been proved that, when the muscle passes into the second form, there results only suppression, or even only diminution, but never

inversion, of the normal current of the muscle under the first form.

C. Rôle of the Muscle in the System: its Function.

Knowing the two forms of the muscle, and the properties which it enjoys under each, we can now form some idea of the manner in which the muscular element works in the organism. The properties of the muscle which are of most use in the system may be said to be:

1. *Its Elasticity.* — We shall see, farther on, that many of the cavities with muscular coats profit more especially by the perfect elasticity of the muscle, and the really wonderful tendency to distension which it shows. With regard to the *stomach* and the *auricles of the heart*, we shall see, in particular, that the muscle, placed in the coats of these membranous bags, is especially useful, on account of the great ease with which it enables these cavities to expand, and we shall have no hesitation in admitting that the muscles (the pulmonary alveoli, for instance, or at least the bronchi) act much more by their elasticity than by their contractility.

2. *The property of passing from the first to the second form* constitutes the real *vital activity*, the essential physiological property, of the muscular element: in this lies its *irritability*. We must, therefore, study this irritability, in order to see if it is really a property of the muscle, similar to that which we have described in the globules; what are the agents which modify it; the irritants which bring it into play; how the muscle responds to these irritants; and, finally, how we can undertake an explanation of the inward changes which then take place in the muscle.

Irritability of the Muscle. — According to the course which we have followed, showing that from the globule; which is the first form of all the tissues and the source of all vital phenomena, the anatomical form and the physiological properties of the muscular element are derived; we can easily conceive that the muscle preserves the same method of irritability as the globule, and that the property of thus reacting, under the influence of excitants, is quite characteristic of it. This has not been the method employed by all physiologists, and, although Haller had already shown *irritability* to be a property inherent in the muscle itself, many authors have since maintained, and maintain still, that the muscle is not *directly irritable* (Funke, Eckhard, Jaccoud), and that all excitants applied to the muscle act upon

it only by the intermediation of terminations of the motor nerves which it contains. Of the numerous facts which refute this theory, and demonstrate the direct irritability of the muscle, we will mention only the two following:

There are certain poisons (woorara) which render the motor nerves completely incapable of action, and, consequently, powerless to convey any irritation to the muscles; and yet, in this case, the muscles which are directly excited can pass from the first to the second form (Cl. Bernard, Kölliker); the ultimate and fine ramifications of nerves which they contain are not affected by this irritability, for the poisons in question deprive of vitality especially the intramuscular terminations of the nerves (Vulpian).

A motor nerve separated from the cerebro-spinal axis loses all excitability after four days: the muscle, on the contrary, previously innervated by this nerve, is still directly excitable more than three months after (if only its connection has been kept up with the sensitive nerves, and the vaso-motors, which provide for its nutrition. Longet).

Variations of Irritability. — This *irritability* belongs, thus, really to the muscle itself, but it is modified by different circumstances, all of which may be said to modify the nutrition of the muscle, or its chemical composition. This is the effect of too prolonged repose. Moderate exercise, which causes a greater interchange between the muscle and the blood, keeps up the nutrition of the muscle, while a contrary effect is produced by fatigue or permanent contraction, by means of which acids accumulate in the muscle, and the alkalinity necessary to the preservation of its properties is lost; thus, a short time after death the muscle ceases to be irritable, the circulation no longer furnishing the materials necessary to its support. The period at which the irritability disappears varies in different animals, being apparently shorter in those whose nutrition is most active; that is, in those whose muscle consumes most quickly the materials left by the circulation: the time being considerably longer in the case of the cold-blooded animals. It varies, however, in an animal, in different muscles, and even in different parts of the same muscular organ: thus the left ventricle of the heart is one of the first muscles to die, while the right auricle keeps its irritability longer than any other muscle of the body, and has thereby gained the name of *ultimum moriens*.

Cadaveric Rigidity. — The muscle, having lost its irritability, passes into the state which we have already spoken of

under the name of *cadaveric rigidity*, which rigidity is owing to the coagulation of the albuminous substance of the muscle (myosin) by the acids which it has formed. The muscle may also pass into the state of *spontaneous rigidity*, after a continued activity which produces great excess of acid: mineral acids, heat 50° c., any thing, in short, which coagulates the myosin, either produces or hastens this rigidity. We have already remarked that an injection of serum or of alkaline liquid entirely prevents or delays it (p. 71). The sort of retraction which the muscles undergo during this rigidity is owing to the contraction or solidification of the coagulated myosin; the muscle is then extremely fragile, and only ceases to be so when the coagulum becomes liquefied by putrefaction. Of course, the muscle then becomes alkaline again by means of the ammonia resulting from its decomposition.

Irritants. — The agents which induce the irritability of the muscle are very numerous. As their mode of action is not exactly known, they have been divided and classed simply as chemical, physical, and physiological.

The *chemical excitants* are very numerous; almost any chemical agent can cause a muscle to pass from the first into the second form. We will only observe that these agents must, in general, be very much diluted, and that some among them, ammonia, for instance, have, when thus diluted, no influence upon the motor nerves, which is a fresh proof that muscular irritability belongs really, not to the nerves, but to the muscles.

Among *physical excitants* we must rank first, electricity, and especially currents, whatever be their source (see p. 30); other physical excitants, often employed in experiments, are pinching, a blow (Heidenhain), or pricking. Most people have seen how fresh meat, in a butcher's stall, will palpitate under the influence of a current of air, a breath of wind. Changes of temperature, especially cold, must also be reckoned among these excitants: cold is often employed in surgery to produce contraction of the smooth muscular elements of the arteries (see circulation; *physiology of the arterial coats*). Indeed, light itself is an excitant of the muscle, as has been shown by Brown-Séquard, in his experiments on the pupil of the eye.

Finally, the *physiological excitant*, whose object in the organism is to make the muscle pass from the first into the second form, is represented by the action of the motor nerves.

Analysis of Contraction.— The muscle, after obeying these irritants, and passing from the first into the second form, returns to the first; this succession of changes is what is called *the contraction* of the muscle. It is made up of several periods: that during which the muscle passes into the second form; the time during which it remains in it; and, finally, that occupied by its return to the first. It has

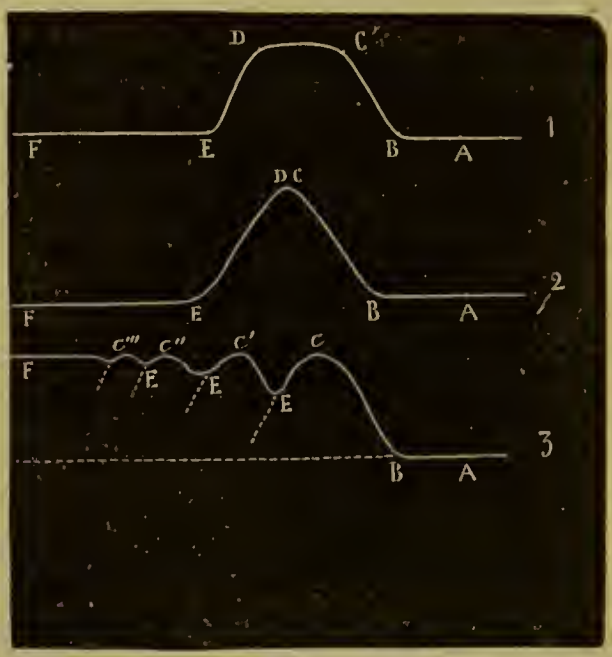


Fig. 20. — Kymo-graphic tracings of muscular contraction *

been also discovered that, when an excitant acts upon a muscle, a short space of time elapses before the latter responds to the excitation (Helmholtz). This forms a period preceding the three others, and is called *latent excitation.*

* 1, Analysis of diagram representing muscular contraction. A B, Latent excitation. B C, Line of ascent. C D, Line drawn during the continuance of form No. 2. D E, Line of descent and return to form No. 1 (E F).

2, Ordinary form of a jerk (*secousse*). A B, Latent excitation. From B to C D, ascent, or passage from form No. 1 to form No. 2; the latter lasts for a moment only in C D, and is immediately followed by the line of descent, D E, or return to form No. 1 (E F).

3, Physiological tetanus. A B, Latent excitation. B C, Ascent. C E, Descent interrupted by a fresh ascent; the jerks (*secousses*) thus produced in succession (c, c', c'', c'''), afterwards succeed each other so rapidly as to become blended in one, causing the muscle to retain the form No. 2, and to describe the line F. The dotted lines indicate the descents or return to the form No. 2, which would take place if fresh excitations did not force the muscle to describe a new line of ascent before it has had time to complete the line of descent produced by the preceding jerk (*secousse*).

If a muscle be suspended vertically by one extremity, having fastened to it at the other a pencil which makes a mark upon a vertical cylinder revolving regularly, so long as the muscle is under the first form a horizontal line will be traced upon the cylinder. Should any excitant act upon the muscle, it will still continue for a certain time to trace a straight line, and this tracing will represent graphically the period of *latent excitation* (Fig. 19, 1, 2, and 3, A B). As the muscle passes into the second form, its lower extremity will trace an ascending line (Fig. 19, B C), representing the passage from one form to the other; at the level attained by this line we shall find that a new horizontal line begins, representing the time during which the second form lasts; finally will come a descending line, representing the return to the first form (D E). The various instruments called *myographs* are constructed on this principle (Helmholtz, Marey); and in this way, also, have been obtained the recorded writings of *muscular contraction*, with analysis of the different periods.

If we examine by this means the contraction of a muscle, which follows a short and sudden irritation (a blow, for instance), we find in the record that the descent immediately follows the ascent (Fig. 19, 2, C D), which shows that the second form has existed only for a short time, and is therefore represented, not by a line, but simply by a point, marking the passage from the ascent to the descent. This is called the *jerk*, or *muscular convulsion.* But when short and sudden excitations succeed each other rapidly, we see, by the diagram, that a new contraction begins before the descent of the first is finished (Fig. 19, 3, c, c', c'', c'''); that is, the muscle, beginning to return to the first form, has been again induced to take the second; these half-descents, interrupted by a new ascent, are therefore marked upon the diagram by a series of undulating lines; they approach nearer the corresponding level of the second form, when these excitations succeed one another more rapidly (Fig. 19, 3, line F). We can easily conceive that the closer the excitations follow each other, the shorter the undulations will be marked, until at length they form a straight line, lasting as long as the excitations continue to take place with the same rapidity; the muscle all this time will maintain the second form.

This preservation of the second form, considered as the result of a succession of jerks (*secousses*) or continuous

convulsions, is what has been called a *physiological tetanus* (Ed. Weber). *Thirty excitations a second* are usually required to produce this. This result leads us to believe that the contracted muscle, as we generally find it in the living animal, remains for a certain time in the second form, only by means of a succession of continuous shocks; in fact, if a muscle in this state be ausculted, a sound is heard, *the muscular tone*, the height of which corresponds to about thirty vibrations a second, which is exactly the number of excitations, and, consequently, of muscular shocks, needed to preserve the second form, or experimental physiological tetanus (Wollaston, Helmoltz).

If, by means of thirty excitations a second, the shocks be rendered simultaneous, producing permanent contraction (or physiological tetanus), and the rapidity of the excitations be then increased, the *force of the contraction increases also;* and, since the tone, or muscular sound, becomes sharper and higher, it is proved that the contraction is composed of a greater number of blended jerks or shocks. This may be easily verified by listening one's self to the sound of the masseter when more or less *strongly* contracted. This sound, heard in the perfect stillness of the night, sometimes rises as high as a fifth (Marey).

If the muscle be fatigued, the shocks are more easily blended together, but the force of the contraction is diminished (Marey).

There are certain striated muscles in which the shock takes place very slowly; in other words, their curve of contraction is very long. Such is the case with the muscles of the tortoise and the muscular fibres of the heart (Marey). The latter forms a sort of transition between the striated and the smooth muscles, the shock of which is very long, and is represented in a diagram by the line of physiological tetanus.

If a weight be attached to the extremity of a muscle at the instant when a shock takes place, or during the physiological tetanus, the weight will be raised, unless it be too great (see pp. 75 and 76). This constitutes the labor of the muscle, and it is in this way that its force is measured.

The *height* to which a muscle can lift any weight depends on the length of its fibres; but what is meant by its *force of contraction* (*absolute muscular force*) is measured by the weight requisite for the neutralization of the movement, and depends only on the extent of the transverse section of the

muscles, or on the number of fibres of which they are composed. Rosenthal discovered, in experimenting on the muscles of a frog, that the contracting force of the adductor muscles in the thigh of this animal varies (in the whole transverse section, that is, one square centimetre) from two to three kilogrammes. In the jumeaux and soleus muscles in man it is about eight kilogrammes to a square centimetre. This experiment is easily made on man. The person to be experimented upon stands upright, and such a weight is placed upon his body as to render it quite impossible for him to rise upon his toes or raise his heels from the ground. At this moment the weight of the body, with the weight added to it, plainly represents the force, or weight necessary to neutralize the movement which the muscles of the calf have a tendency to produce when the person rises upon the toes, or, better still, on the extremities of the metatarsals. The exact force of the muscles of the calf is thus equal to the value of this weight divided by the length of the lever arm (see farther on, *mechanism of the skeleton:* lever of the second kind); given, then, the mean transverse section of the muscular mass of the calf (gemelli and solears) it is easy to deduce from it the exact force of the whole surface of these muscles.

The total weight of the mass of the muscles in man shows that, in a mechanical point of view, these organs form machines quite powerful and perfect; and that, in proportion to their weight, which is comparatively very light, they develop a much greater force than any machine that we can construct.[1]

Physiologists have analyzed still more closely the phenomenon presented by the passage from the first to the second form, and have sought to discover the molecular modifications which take place in the muscular fibre during this phenomenon.

It is scarcely worth while to mention the theory which explained the second form as being a zigzag folding of the muscular fibre (Prévost and Dumas, 1823), this theory having been proved to be founded on an error in observation. In this case the muscular fibre, being placed upon a sheet of glass, adhered to it by its sheath, so that, after taking the second form, it could not easily return to the first, its adherences causing it to bend in a broken line; it is then

[1] Weber, Rosenthal, Hermann.

only, in this incomplete return, that the zigzag form is observed.

Two theories now contend for the explanation of this phenomenon.

According to some (Weber, Aeby, Marey), the almost liquid contents of the muscular fibre are the seat of a series of waves (*muscular wave*), whose presence produces the shortening of the muscle, and its transverse enlargement.

According to others (Rouget), the muscular fibres are decomposed into smaller and very numerous *fibrils*, formed by a sort of *spiral line*. As the juxtaposition of these spiral lines explains the striated appearance of the muscular fibre, so their lengthening or shortening gives us the key to the first and the second form, and to that caused by the passage from one to the other.

Marey has shown that if two of those myographical pincers, which are used to register the swelling which takes place in a muscle when contracted, be placed at a certain distance from each other lengthwise upon the muscle, these two pincers will not record the swelling of the muscle at the same instant; the one nearest the extremity which is excited acts first, and then the other. The swelling of the muscle thus advances like a *wave*, of which the velocity has been estimated by Marey at one metre a second. Aeby has, however, shown that if, instead of exciting the muscle at one extremity only, it be excited throughout, by placing each extremity in contact with one of the wires of the exciting current, or if the motor nerve of the muscle be excited; the two tracings made by the myographical pincers are exactly superposed or synchronic. In this case the muscular fibre contracts in all its parts at once.

Professor Rouget has observed, by examination of the contractile pedicle of the vorticelli, that the muscular fibre is a true *spiral spring* (p. 68), *which, actively distended during the repose of the muscle, returns upon itself at the moment of contraction:* muscular contractility is a purely physical property of elasticity; the rigidity of a corpse is a phenomenon of the same order as muscular contraction in the living body. "The *stem of the vorticella* presents the principal organ of locomotion of an animal, formed by a single muscular fibril, free in a tube, at the centre of a perfectly transparent sheath; which allows us to see with the greatest distinctness all the changes undergone by the contractile element during its state of activity or of repose, of elongation or of con-

traction. When the animal is at rest the style is at the maximum of elongation, and the body as far as possible from the points of adhesion and of refuge. In this state the central filament of the style, the contractile fibril, is completely extended; it is, however, never straight, but always twisted in a long spiral line, like a ribbon wound round its longitudinal axis; which resembles exactly the spiral spring of a watch, fixed and firmly drawn out at the extremities.

"At the instant that any mechanical, electrical, or thermical excitant touches the animal, this elongated spiral line, returning suddenly upon itself, is transformed almost instantaneously into a spiral spring of perfect uniformity, the coils of which are very near each other, measuring not much more than a fifth of the length of the style when in repose, while their transverse diameter is proportionately increased. This state lasts generally only for a short time; the coils of the spring withdraw from each other, the spring lengthens out slowly, and the animal returns to its former position.

"The shortening or lengthening of the contractile organ is here evidently owing to the junction or separation of the coils of a spiral spring. But which of these two states is that which brings the elasticity into play? In which do we find the muscular spring returned to its natural form, the state of repose? In the first place, observation has established this important fact, that the spiral filament is never found at its extreme elongation unless the animal is alive and uninjured. If the animal be killed, or the style detached, the coils of the spring roll up into a tendril, and remain in this state: the case is the same if the animal be killed by any poisonous agent, or by raising the temperature to + 40 or 45° (C). It frequently happens, during the lifetime of the animal, that the contractile fibril is severed, and thus the continuity between it and the body, or the trophical centre of the whole animal, broken: in this case, although the sheath is perfect, the body, living and swimming by means of the vibratile cilia, drags at its inferior part the dead contractile fibril, rolled up like a tendril, having for ever lost the power of further elongation. The lengthening of the spiral fibril, the organ of muscular movement in the vorticellus, belongs thus to the living state, that is, to the continuance of nutrition and exchange of matter. As soon as nutrition has been stopped by the death of the animal, or by the separation of the fibril from the trophical centre, the contractile element

takes and keeps the form naturally belonging to its structure, which is that of a spiral spring, the coils of which, when in the state of repose, are as near as possible to each other.

"The contraction of the muscular fibre of the style of the vorticellus corresponds with the state of repose of the spring, and is the direct consequence of its elasticity; the lengthening of the fibre is the result of the forced extension of the spring, by means of a movement connected with the act of nutrition, and acting during the apparent repose of the contractile organ. When the source of this antagonistic force is dried up, the elasticity, by bringing the muscle back to its original form, produces the said contraction. . . . The tendency to a state of extreme contraction is thus an inherent property of the living muscular fibre, a necessary result of its structure and of its elasticity. During life this tendency to shorten is combated by an extending cause which prevails during the repose of the muscle, and is developed in the change undergone by the elements of nutrition, increasing as these are more abundant, diminishing or disappearing in their absence; and it may be momentarily suspended by any of the excitants of muscular contractility, such as nervous action, heat, a blow, etc."

In another series of investigations Professor Rouget, experimenting on the living animal, has shown that any thing which is an obstacle to the nutrition of the fibre causes it to contract. By tying the artery of a limb, and constantly increasing the excitations by the application of increasing heat, he found that he obtained always the same results. According to him, the effect of too frequent repetition of an excitation, such as excessive heat, is to stop the progress of nutrition. In both these cases the *myograph* (see p. 84) has shown that the contractions of the fibrils, becoming more frequent, at length follow one another so closely that there is no longer any interval between them, and the muscle then enters into the state of tetanic rigidity. Thus: "the tendency to shorten, which is the result of the peculiar elasticity of the muscular element, is permanent. During life and the repose of the muscle it is combated by a tendency to lengthen, the energy of which is in proportion to the activity of nutrition, and expires with it. Contraction takes place at the moment when the equilibrium between these two opposite tendencies is broken by the withdrawal of the extending power. As the coefficient of elasticity varies in the living muscle with the different states of repose, contraction, and rigidity, so

these variations modify the form and energy of the contractions. The movement by which, at the moment when contraction takes place, the labor of muscular extension ceases, is shown under the form of an increase of temperature. The shortening is the effect of the peculiar and permanent elasticity of the contractile spiral line; the lengthening is produced by a moving cause which is developed in the act of nutrition, and is correlative to heat, if it be not heat itself."[1]

It seems certain, as we have already said, that we must place the change of form of the muscle in the general class of physiological phenomena. We know that one of the essential properties of the globules is this power of change of form: the muscular fibres are derived from the globules, and have kept this property in a very striking degree, as well as the other properties which we have already studied (elasticity, electro-motor power, chemical changes, etc.) The following experiment by Kühne confirms this view of the subject, by which, without offering any theory as to the phenomenon, we at least include it among the general properties of essentially living elements. By filling a fragment of the intestine of an insect with protoplasm of the *myxocimetes* (cryptogamous plants, composed only of extremely contractile globules of pure protoplasm), he formed an artificial muscular fibre, having an envelope and contents, and presenting, under the action of excitants, all the appearance of a real muscular fibre, that is to say, passing from the first to the second form.

As with the globules, however, it does not appear that the change of form takes place at once in the whole extent of the muscular fibre. If we examine a certain portion of a fibre with the microscope, we find the change of form at first local, and then spreading immediately, like a wave, along the fibre. This experiment, which is easily made on the muscles of insects, especially on the long slender legs of the spider (in which the contraction of the muscular fibres may be observed through the animal's transparent tissue), confirms what we have already quoted from Aeby and Marey (p. 88), as to the *muscular wave*, as demonstrated by means of the myographical pincers.[2] In it we make use, not of the

[1] Rouget, "Académic des Sciences," June, 1867.

[2] For an interesting, as well as instructive, account of the changes of form of muscular fibre during contraction, as seen in a muscle attached to a living animal, and viewed under the micro-

change in length of the muscle, but of its change in thickness, by enclosing it in a kind of pincers, one of the movable branches of which (myographical pincers, Marey) operates on a registering apparatus. Of course, we find the same simple shocks, or elementary contractions, and the same fusion of these shocks in physiological tetanus, as with the former method, but the process is more practical, and may be made use of, for instance, to register the contractions of the biceps in man.

III. Smooth Muscles.

The *smooth muscular* fibres (Fig. 21) are situated chiefly in the coats of the viscera (intestine, bladder, uterus, etc.), or in the tubes which open into or proceed from them (the bronchus, ureters, urethra, bile duct, etc.). It is thus difficult to form a distinct group of this contractile element, for the purpose of making it a special study.

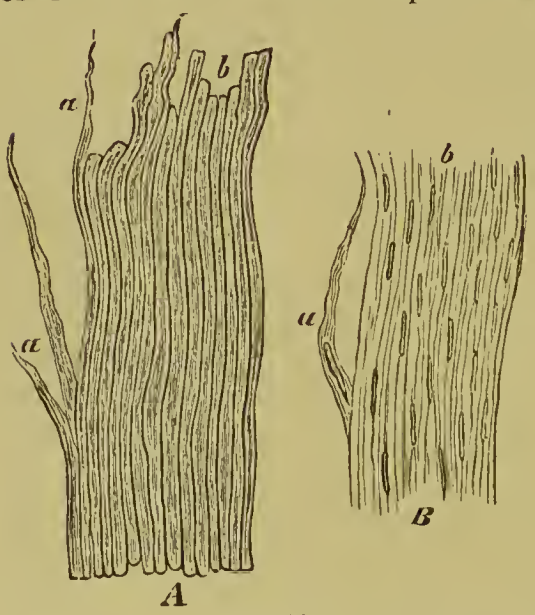


Fig. 21.
Smooth muscles (of the wall of the bladder).*

Still, by studying the smooth muscles as we find them with all the normal intricacies of their fibres, we are easily convinced that these elements, like the striated fibre, possess the property of appearing under two different forms, which we may still call *first* and *second.*

The smooth muscle appears to possess, under these two forms, the same properties as the striated muscle under similar forms, as well in regard to its *chemical reactions*, as to

scope, the reader is referred to a monograph by Professor Thomas Dwight, Jr. (Boston Nat. Hist. Soc. Proceedings, Nov. 5, 1873.)

* A, A fasciculus, from which proceed, in *a*, *a*, detached cell fibres. *b*, Represents it in section. B, A similar fasciculus, having been exposed to the action of acetic acid: the nuclei appear long and slender. *a* and *b*, as above. 300 diam. (Virchow, Pathologie Cellulaire.)

the *electro-motor force*, *elasticity*, and *respiratory exchanges* (combustion). But what distinguishes the smooth muscle from the striated muscle is that in the former the passage from the first to the second form is made with *extreme slowness*. After the excitation which irritates the fibre, and gives rise to its change of form, a considerable time always elapses before the change occurs. As this *latent excitation* lasts a long time, so the *contraction* which follows is produced very slowly, continues for some time at its height, and then gradually relaxes.

Thus, the only consequence of the difference in structure of the smooth muscles is that they *yield less readily to the influence of irritants*, and *contract more slowly* than the other muscles. They also pass into the state of *cadaveric rigidity* in the same manner as the striated muscles. A state of transition between the striated muscles and the smooth muscles, properly so called, is also sometimes observed. This is the case, up to a certain point, with the muscular tissue of the heart. (See p. 86.)

On resuming a series of investigations as to the comparative physiology of the smooth and the striated muscles, M. Legros and M. Onimus arrived at the following conclusions: in the case of the striated muscles both the contraction and the return to a state of repose are rapid, while in that of the smooth muscles both are slow. These movements are always *involuntary*. The *contraction* (physiological tetanus) of the former is caused by a series of shocks, while that of the latter comes on gradually, without oscillation. The *peristaltic form* (see intestine) is that in which these contractions most frequently appear. The *motility* (excitability) lasts longest in the smooth muscles after death. In the striated muscles electrical excitation of the motor nerves of the muscle produces more effect than that of the muscle itself; with the smooth element the reverse is the case. Finally, if the two poles of an induced current be made to act upon the smooth muscles, by placing these poles at a certain distance from each other, we find, in the intestinal tube, for instance, that instead of the whole muscle contracting, those parts only contract which come in contact with the poles; in the intermediate parts there is no contraction, but rather relaxation. The effect produced by continuous currents is still more remarkable: in those organs which have peristaltic movements (see *intestine; vaso-motors*) there are variations corresponding with the direction of the current; when this

follows the direction of the normal peristaltic contractions, relaxation takes place, while if it goes in a contrary direction, contraction is produced.

IV. Contractile Cells.

The different properties of the *contractile* cells resemble closely those which we have studied in the cells in general, especially the faculty which they possess of changing their form. This property being common to the whole mass of protoplasm, we will here, after speaking of the muscle properly so-called, mention only those contractile cells which are of special use in the system, on account of their *contractility* or *irritability*. Now these elements are to be found scarcely anywhere fully developed, except in the arteries, — in the smaller arteries especially. Thus, in order to study the functions of these embryonic muscular forms, we must examine the small vessels. (See circulation.)

Among the movements which take place in the cells, we must also mention the *movements of the vibratile cells*. We shall speak of these in reference to the cylindrical epitheliums which are found to have this ciliary covering.

V. Adjuncts of the Muscular System.

(Connective Tissue, Bones, Tendons.)

General Mechanism of the Muscles. — The muscular fibre, in changing its form, plays an important part in the system as the source of labor and of movement. For this purpose it is in close relation with other organs, and exhibits two different tendencies, acting either by compression or by traction.

In the former case (*pressure*) the muscular elements are arranged in the form of handles or rings, or even of membranous pouches, in such a manner as to compress on all sides the organs which they enclose. The sphincters, the muscular tubes (pharynx, œsophagus), and the heart, as well as all the *hollow contractile organs*, are formed according to this plan. Nearly all the muscles of the *organic life* (smooth muscles) exhibit this arrangement. Their function is, generally, to further the passage of the liquid, or, at all events, *softened* matters, into the interior of the reservoirs and tubes of which they form the walls, and they attain their end by

means of the unequal pressure which they produce in these reservoirs, liquids having always a tendency to move towards the point of least pressure. (See *movements of the stomach, of the intestine, the bladder, uterus*, etc.)

In the latter case the muscular fibre is inserted in the organs which it is intended to affect, in the levers which it is to move (bones) by the medium of resisting cords (tendons). The study of the *ligaments* belongs to that of the *bones* (and of their articulations); the study of the *aponeuroses*, to that of the *tendons* and the *muscles*. The bones,

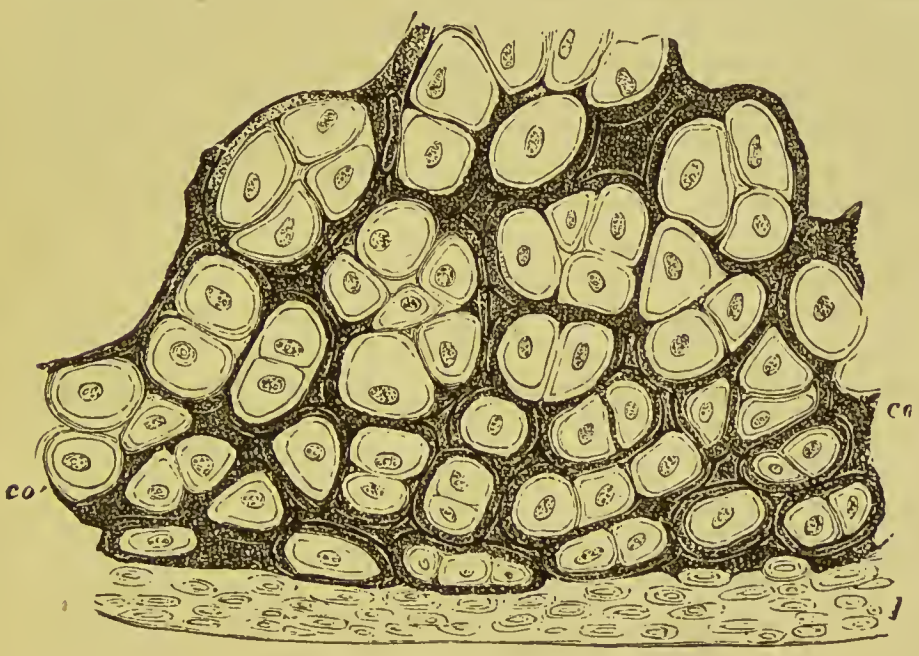


Fig. 22. — Section of cartilage.*

the articular cartilages, the ligaments, the tendons, the aponeuroses, thus constitute the *passive organs of locomotion*. The tissues of these organs are so associated in histological and chemical peculiarities, that they have been classed together, and form a vast family, called *group of connective or collagenous tissue*. The tendons, the aponeuroses, the ligaments, and the connective substance of the organs form the *connective or cellular tissue*, properly so called.

Connective Tissue, properly so-called. — This tissue has

* c, c, Calcified cartilage. c′, c′, The calcareous salts are just beginning to be deposited. p, *Perichondrium*. 350 diam. (Virchow, "Pathologie Cellulaire.")

the closest connection with the muscular element, and it is this which, under the names of *perimysium* and enveloping aponeurosis, unites the muscular fibres in clusters or masses of flesh, so as to admit of united action on the part of the contractile elements; but this tissue is found to be distributed, not only in the muscles, but throughout the other organs: it was formerly called *cellular tissue*, but this name is inadequate, for it expresses only a general disposition of the tissue, by means of which it is easily penetrated by the gases or liquids which it encloses in *vacuoles* or *cells* (in the *macrographic* sense of the word). The whole body may be looked upon as a mass of connective tissue, or of one of its different forms, in which the more essentially active elements are located. Thus, this tissue has a large share in the composition of the nervous centres, prevailing even over the nervous tissue, properly so-called; and the knowledge of this

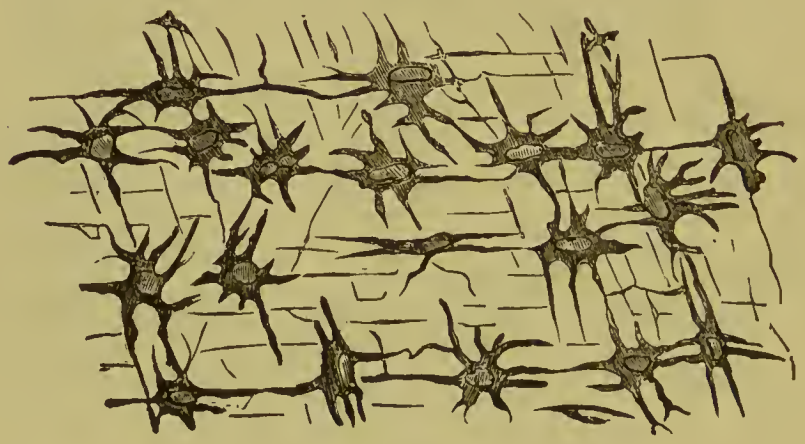


Fig. 23. — Plasmatic cells of the cornea.*

fact has lately given rise to entirely new views as to the nature of diseases of the cerebro-spinal centres, and even of the nerves in general; as, for instance, in sciatic neuralgia, in which the pathological change is generally produced in the cellular tissue of the sciatic nerve.

The connective tissues are generally rich in *embryonic* or plasmatic globules (see above, p. 21), or their derivatives: cartilaginous cell, bony cell (Figs. 24 and 25). In some places these globular elements appear to have a certain

* The cornea is here cut parallel to its surface. The star-shaped corpuscles (embryonic globules or plasmatic cells) are seen flattened out, together with their anastomotic prolongations (*Iris*).

part to play, as, perhaps, in the intestinal villosities; and here they may possibly have some share in the labor of absorption; they may, besides, by being filled with fat, serve as a reservoir for this substance, as in the *panniculus adiposus* (subcutaneous areolar tissue) of a child. But in general the globular element of the connective tissue takes an important part only in pathological phenomena, when, under the influence of a more or less direct excitation, it proliferates and gives rise to the production of pus and various new formations.

Even in the case of the connective tissues which have the fewest plasmatic globules, the latter, in pathological conditions, are largely developed. When the aponeuroses, for instance, are the seat of suppurations, we find them transformed, by proliferation of the plasmatic cells, into a simple mass of globules. The fewer plasmatic cells there are in a connective tissue, the less tendency it shows to change under the influence of pathological causes; thus the tendons, which are comparatively poor in globular elements, are slow to yield to the process of suppuration.

The globular element of the connective tissue, properly so called, as well as of its derivatives (collagenous tissue, bones, cartilage, etc.), being important only in pathology, may be almost disregarded in physiology. In respect to the organs which are formed essentially of these tissues, we need, therefore, consider only some of their physical properties and mechanical uses, which are due to the nature of the fundamental substance in which the plasmatic cells are imbedded.

These physical properties are very different from each other, and are sometimes antagonistic, though found in very similar forms of connective tissue: as, for instance, the *rigidity of the bones*, and the *elasticity of the ligaments*.

The Bones. — The bones are formed of lamellæ, enclosed one within another, imbedded in calcareous salts, and surround canals containing the spinal cord. This latter, formed almost entirely of embryonic globules, must be considered as living, unless the globules have completely passed into the state of fatty degeneration. In a purely physiological point of view, however, the bony lamellæ show scarcely any trace of life. It is true that the bones contain, in the calcareous lamellæ, some globular elements (such as bony corpuscles, bony cells) which are similar to the plasmatic globules (Fig. 24); but there is little evidence of their receiving nutrition, and they are of importance only in pathology. It

is also true that the bones grow; embryonic globules may be seen, in their circumference, in course of proliferation, some bony parts disappearing, while others make their appearance. They are simply changes of form, if we look at the skeleton as a whole, but insignificant, if we consider this element in particular; and, in the adult stage, the bony lamellæ have only physical properties. What is true of the bones is also true of the cartilages, which are really bones, only less rigid and more elastic than what are usually called by that name.

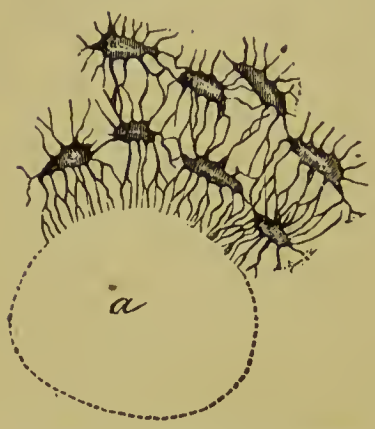


Fig. 24. — Histological elements of the bones.*

Tendons and Ligaments. — The tendons and ligaments are composed essentially of wavy or undulated fibres, sometimes interlaced with each other, but which give no appearance of change of form, so that we may almost decline to consider them as living. The part which they play is entirely mechanical, and belongs to their powers of resistance and elasticity. We find the latter property developed in the highest degree in the *yellow elastic tissue*, which is a non-collagenous variety of connective tissue; the elastic fibre is still more undulated than the cellular fibre; it is exceedingly curly (Fig. 25, *b* and *c*), and, when stretched out, makes great efforts to regain its original form: the *yellow* or *elastic* ligaments also serve to bring the different parts of the skeleton back into their normal positions, when they have been disturbed by muscular action, whence the name which is sometimes applied to them, *passive muscles*. We find this elastic element always at work in the arteries, simultaneously with, and in opposition to, the muscles; and thus the result of this incessant antagonism is the uniform circulation of the blood.

In general, wherever it is possible, yellow tissue takes the place of muscle. This element, which acts like a spring, is not alive, and does not, like the muscle, require nourishment, whence there ensues great economy to the system (e.g., the cervical ligaments of the large carnivora, the yellow ligaments of the vertebral lamina, the yellow ligaments in the

* Transverse section of part of bone enclosing a Haversian canal (*a*). Bony corpuscles, with their anastomosing prolongations. 300 diam. (Todd and Bowman, "Physiological Anatomy of Man." London, 1845. Vol. 1, p. 109.)

wing of birds, in the wing of the bat, etc.). These parts, however, do not require to be frequently renewed, whence the great difference between the connective tissue of old and young people, and the stiffness in motion and frequent fractures which we observe among the former.



Fig. 25. —Elements of connective tissue: connective and elastic fibres.*

The tendons are, in a mechanical point of view, only soft and flexible apophyses or simply appendages. Their use is to enlarge the surface of the bones, so as to admit of the insertion of a greater number of fibres. Whenever one of these apophyses is in danger of becoming too long, and by its consistency and its position would interfere with the mechanism of any member, it becomes a *tendon.* We find certain apophyses, the styloid apophysis, for instance, which is some-

* *a*, Connective fibres, having some embryonic globules. *b*, Elastic fibres, with their anastomoses and divisions. *c*, Curly elastic fibres (like horse-hair in a mattress). *d*, Nuclei of cells, with nucleoli, taken under the pectoral muscle. 320 diam. (Todd and Bowman, "The Physiological Anatomy of Man." London, 1845, p. 74.)

times bony, and sometimes tendinous; while, what is tendon in man becomes bone in certain animals. In reptiles, for example, the *linea alba* becomes a bone, and the intersections of the *recti* muscles are represented by as many distinct bones. In birds the tendons are represented in certain parts by bony stems, placed along the extended portions of the principal bones. The existence and length of the tendons depend on the nature and extent of the motion to be produced. Whenever this is of great extent, and requires great strength, muscular tissue is predominant throughout the muscular apparatus, and is directly inserted into the bone. Wherever the movements of the bony parts are of small extent, and require only a slight shortening of the muscle to produce them, we find the fibres of this muscle short, and ending in a true tendon.



Fig. 26.*

The force of a muscle is usually estimated by the number of its fibres, that is to say, by its thickness and by its diameter (see p. 87). The length of a muscle, on the contrary, corresponds with the degree of displacement of the bones (compare the sartorius and the muscles of the thenar). We find some short muscles, placed at great distances, and yet, compared with one another, possessing slight degree of movement. In such a case as this, a tendon takes the place of a large part of the muscle, as in the case of numerous muscles of the forearm, in which the muscular parts are short, and the tendons very long: a greater length of muscular fibre would be unnecessary here to produce such a slight displacement as the flexion of the hand upon the forearm, and of the phalanges against each other. The *extensor cubital* muscle appears to be an exception to this rule; but, in reality, although its fleshy part occupies the whole length of the

* *e*, *f*, *g*, *h*, Embryonic globules of connective tissue. Relation of these elements (plasmatic) to fibrous tissue (*Schwann*).

forearm, its muscular fibres are very short, being placed obliquely, and constituting a demi-penniform muscle, extending from the os cubitus to the tendon, which runs the whole length of the forearm.

Sometimes the sinewy intersections, which are placed along the path of a muscle, have a special part to perform: thus the intersections of the rectus of the abdomen divide this muscle into as many distinct muscles, thus providing for partial contractions, which would be impossible in a long muscle made entirely in one piece: the same may be said of the numerous digastric muscles in the neck, and of the nape of the neck (grand complexus, etc.).

Mechanism of the Bones, considered as Levers. — In the play of the muscles, of the tendons, and of the bones we find mechanical apparatus exactly similar to the three kinds of levers.

The *lever of the first kind* is to be often met with in the animal economy. In the case of man we might call it the

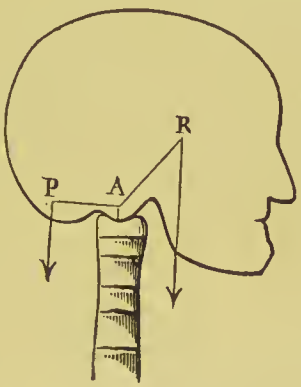


Fig. 27. — Showing the equilibrium of the head upon the vertebral column.*



Fig. 28. — Diagram of the foot and ankle, the heel being raised by the tendon of Achilles (Dalton).

standing lever; for it is in the equilibrium of the erect posture that we find the greatest number of examples of it, and it is very rare to find this kind used for movements of the body. When the head is in equilibrium upon the vertebral column, in the occipito-atloidean joint (Fig. 27) it represents a lever of the first kind, the *point d'appui* of which is its junction with the vertebral column (in A). The *resistance* (weight of the head) lies in the centre of gravity of the

* Lever of the first class. A, Fixed point. R, Resistance (centre of gravity of the head). P, Force (the arrows indicate the direction in which the force and the resistance act).

head, that is to say, above and a little in front of the centre of motion (in R). The *power* is represented by the muscles of the nape of the neck, inserted in the lower half of the occipital (in P). By uniting these different points we obtain a bent lever of the first order, which can be easily transformed into a direct lever. We see the same thing exemplified in the preservation of the equilibrium of the trunk upon the heads of the two femoral bones: the coxo-femoral joints form the leaning-point of a lever of the first order, in which the resistance (centre of gravity of the trunk) is placed behind, and the power (anterior muscles of the thigh) is placed before. A similar lever is found in the articulation of the thigh with the leg, and of the leg with the foot (in the *movements of equilibrium to maintain the erect position*).

The two other kinds of levers are to be principally found, not in the equilibrium of standing, but in the movements of locomotion.

The lever of the second kind, or *inter-resisting* lever, in which the arm of the power is longer than the arm of the resistance, and in which, consequently, speed is sacrificed to strength, is found in man only under *two circumstances*, — when the upper part of the trunk is raised by pushing with the palms upon a resisting plane, and when the whole weight of the body is raised by standing upon the points of the toes, which happens at each step, in the movement of walking,

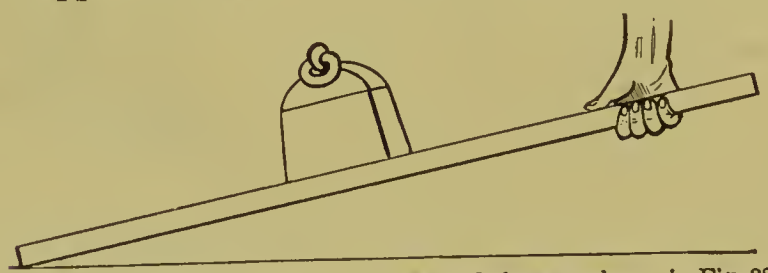


Fig. 29. — Example of a lever of the second class, as shown in Fig. 28. (Dalton.)

at the period when the foot, leaving the ground, oscillates in the air, and places itself before the other. In this case (Fig. 28) the *point d'appui* is upon the axis of the transverse cylinder, formed by the junction of the series of metacarpal bones with the phalanges. The power is represented by the muscles of the tendo Achillis, and its point of application is found in the posterior extremity of the os calcis. The resistance, that is to say, the weight of the body transmitted by the tibia, lies in the upper facet

of the os calcis, and of the astragulus (forming a single bone in movements of this kind), at the level of the tibio-tarsal joint, and, consequently, between the fixed point and the point of application of the power. The lever arm of the power is thus longer than the arm of the resistance; and, consequently, the power to raise the body, displayed by the muscles of the calf, may be inferior to the weight of the body itself, as is shown us by the law of levers of the second kind (Fig. 29).

The *lever of the third kind* (power between fulcrum and weight) is the most common; it is the lever of locomotion *par excellence:* we find it in most partial or complex movements, and especially in the movements of flexion and extension. We need not examine the shoulder and elbow joints in the act of prehension, in order to establish the type of this lever, for here the arm of the power is always shorter than that of the resistance, so that the energy of the muscular contraction must always be superior to the resistance to be overcome. Yet, on the other hand, the distance traversed by the resisting extremity of the lever (the hand, for example, in the flexion of the forearm) is greater than that traversed by the point of application of the force (insertion of the biceps in the upper part of the forearm); and thus what is lost in power is gained in extent.

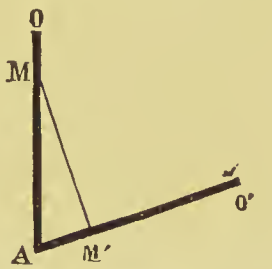


Fig. 30 — Diagram of the elbow, as a lever of the third class.*

The working of these different levers is facilitated by the disposition of the bones, in which a deep cavity is hollowed out (cancellated texture), filled with a soft and almost liquid matter (marrow). By this arrangement the weight of the bony levers is diminished, while the bone affords a surface sufficiently large for the insertion of the numerous muscles by which it is moved. The substance which fills these cavities is the lightest in the whole system, — fat (marrow, in the adult). Finally, this arrangement of the bones is favorable to the part which they play as supports, for mechanics teach us that of two columns of the same height, and *formed of an equal quantity of matter*, one being solid and the other hollow, the latter will be the stronger. This principle ap-

* O, A, Humerus. A, O′. Forearm. M, M′, The biceps. — As a lever: A, fixed point; O′, point of application of the resistance (the hand); M′, point of application of the force.

plies to the hollow columns formed by the bones of the different members; that is to say, given an equal quantity of bony substance, these organs, being filled with little canals (canaliculi), offer greater resistance than if they were solid, and thus combine strength and lightness.

The bones are not merely rigid levers, necessary to motion; we have now seen that they serve as columns or supports in standing, intended to sustain the weight of the body. They form also a more or less complete scaffolding for the protection of certain cavities, such as the ribs, the pelvis, and especially the skull, which supplies an incompressible covering to the brain.

The Joints. — The parts by which the different pieces of the skeleton are united are called the joints. The joints are thus, generally, the centres of motion; they are also placed in such a manner as to avoid friction as much as possible. The *cartilages*, which cover the surface of the joints, are compressible and elastic, and thus form protecting cushions which serve to moderate shocks, to diminish friction, and to resist pressure in the different movements of locomotion, and in the equilibrium of the erect posture. They are lubricated by a *synovial* fluid, which is a ropy and unctuous substance, and, at first sight, resembles the white of egg, but which, by its properties, partakes rather of the nature of *mucus*, properly so called. Indeed, as is the case with all mucus, the synovial fluid is the result of the liquefaction of an epithelium which lines the inner surface of the articulating capsule. The movements and friction between the articulating surfaces have great influence on the composition of the synovia; when the animal is in repose this fluid is very watery, less sticky than at other times, and contains little cellular waste. After long and active exercise it becomes thick and sticky, containing a larger quantity of *synovia*, or *mucine* (see physiology of the mucous surfaces: epitheliums), and of epithelial waste (Frerichs). The synovial fluid thus possesses great power of cohesion, and adheres firmly to any surface which it bathes. Strictly speaking, it is not the cartilages, but these liquid coats, which come in contact with each other, so that scarcely any friction ensues. It is only in some cases of disease that the synovial fluid disappears, and consequent attrition occurring, causes rapid atrophy and destruction of the adjacent layers of cartilage and bone.

Around the joints, beside the articulating capsule and its

synovial epithelium, are found parts which are formed of resisting fibrous tissue, called *articulating ligaments*. Outside the joints again, and around the muscles, are found other fibrous and membraniform apparatus, called aponeuroses. The object of these two apparatus is not so much, as is generally supposed, to keep the articulating surfaces in contact, as to limit the extent of the movements of the joints. The ligaments which immediately cover the joints act as *resistance*, with a lever arm which is too short, and would not be able to regulate the movements, were they not aided by the aponeuroses, which are a kind of ligament placed farther off, and, consequently, more powerful. Thus, in the aponeurosis of the thigh, the *fascia lata* is only a *ligamentous bridge* thrown from the pelvis to the leg, thus belonging to the coxo-femoral and knee joint; it is intended to prevent too great mobility in the inferior limb. This fascia, though less strong than the articulating ligaments, exercises in this way a much more important influence, because, being placed at a great distance from the centre of motion, it acts with a much longer lever arm. The case is the same with the *cervical aponeuroses*, which are only ligaments, intended to prevent the too great inclination of the head either backward or sideways: here, again, these are only membranes, weak in themselves, but which become powerful by the length of their lever arm.

There exist, however, a certain number of aponeuroses and ligaments, the use of which is evidently not the regulation of the movements of the joints: such are the aponeuroses of investment, which prevent any deviation in the muscles during their contraction. Others, as the annular ligament of the wrist, serve as *pulleys of reflexion* for the flexor muscles. Others take the place of bones for the insertion of the muscles: such are the *interosseous ligaments* of the forearm and of the leg, the abdominal *linea alba*, etc. On the other hand, the *sclerotic coat*, an essentially fibrous membrane in the eye, is intended to preserve to the eye its spherical form, which form is necessary for the preservation of the optical properties of this organ. In general, the principal use of the fibrous tissue is the part which it plays in reference to the joints.

The *ligaments* serve to keep the bones in contact only when they are situated between two bones, as in the case of the *symphises*, thus uniting two parts of the skeleton which

have little motion. But in the movable articulations (diarthroses), the ligaments, situated principally in the periphery, are powerless to prevent the disturbance of the articulating surface, as may easily be seen in the scapulo-humeral and coxo-femoral articulations, where the heads of the bones may be considerably displaced from the socket, in spite of the perfection of the ligamentous system. In joints of this kind it is simply *atmospheric pressure* (Weber) which produces the adhesion of the articulating surface. A dead body may be suspended, the lower limbs hanging freely, and we may then remove all the soft parts, skin and muscle, which surround the coxo-femoral joint; the articulating capsule may then be cut, and the limb will still remain suspended from the cotyloid cavity: an additional weight may even be superimposed without destroying the adhesion; but if, by an opening made in the lowest part of the cotyloid cavity, the air is allowed to penetrate the articulating surface, the adhesion ceases instantaneously, and the head of the femoral bone quits its socket. If the bones be then replaced, the air which has entered be expelled, and the opening previously made be stopped up with the finger, the limb will again remain suspended as long as the air is kept out (experiment of the brothers Weber). It is thus the *vacuum*, or the close contact of surface, which allows the atmospheric pressure to act as a counterpoise to the limbs, that are thus supported without any aid from the muscles.

When, by stretching the fingers, we succeed in slightly separating the phalanges, a well-known crackling sound is produced, of which the foregoing study supplies an explanation: the stretching of the joints of the phalanges overcomes the pressure of the atmosphere, and separates the articulating surfaces which were kept in contact by it; but, at the moment of separation, the soft peripheric parts are thrown by the same pressure into the space between the two bones. These phenomena are very sudden, and give rise to sonorous vibrations, whence the crackling sound.

The preceding remarks on the mechanism of the bones, of the muscles, and of the tendons, help us to understand the different kinds of labor and the different movements of which man is capable. We need not examine the action of jumping, of climbing, of swimming, etc. We will only consider, for a moment, the ordinary *walking step*, the brothers Weber having shown that in this mode of progression each

of the two legs is alternately thrown forward by an oscillatory movement exactly similar to that of a pendulum.

Let us suppose a man stopped in the act of walking: he has just completed one step, and stands upon his two legs, the left, for instance, being placed before, and the right behind. To continue his walk, to make a new step, what happens is as follows: the left leg, which we will call the *active leg*, is placed perpendicularly upon the ground, and forms the right side of a rectangular triangle, of which the hypothenuse is formed by the right leg, stretched out behind; the right leg, we shall see, may be called the *passive leg*. The left or *active* leg, at first slightly bent, is then extended, and carries the pelvis forward and upward. To produce this effect the heel of the left foot is raised from the ground by means of the mechanism which we explained *à propos* of levers of the second kind, and the limb now leans only upon the extremity of the *metatarsus*. During this movement the right or passive leg, being forced to follow the forward movement of the pelvis, is passively detached from the ground, and makes a forward movement, like a pendulum, around its point of suspension to the pelvis, by which the right foot is carried as far before the active foot (the left) as it was previously behind it; it is then placed upon the ground, and the movement, by which the active leg (the left) throws forward the pelvis, being continued and finished, the right foot finds itself at last placed perpendicularly upon the ground, as was the left foot at the beginning of the step. The step which we have been considering is finished, and in the new one which follows the same takes place, the parts only being reversed: the right leg becomes the active one, the left the passive.

In short, the walking step may be represented by a rectangular triangle which changes its position, the sides moving in such a manner that the one which represented the right side at the beginning of the step (the left leg in the preceding example) passes into the position of the hypothenuse, and *vice versâ*. The leg which, from the right side, passes into this position *is all the time active*, while the leg which passes from the position of hypothenuse into that of the right side *is all the time passive*, and *oscillates in the same manner as a pendulum*. In order to oscillate without touching the ground, the passive leg must be slightly shortened; this takes place without any aid from the muscles of

the leg. Indeed, the inferior limb represents, in oscillating, a double pendulum (the thigh on one side, the whole of the limb on the other). It is well known that the law of oscillation in a pendulum is that a pendulum composed of two parts united by a joint bends slightly in the joint as soon as it begins to swing.

Some physiologists, however, deny that the leg which we have called passive is entirely passive; they maintain that it undergoes a slight degree of contraction of the flexors, precisely in order to produce the flexion necessary to the oscillatory movement. Duchenne (of Boulogne) draws, from his pathological observations, the conclusion that the oscillatory motion of the leg would be impossible, without the contraction of the flexors of the thigh upon the pelvis, of the flexors of the leg upon the thigh, and of the flexors of the foot upon the leg.[1] It is difficult to decide on this subject, for some authors here bring in the question of *muscular tonicity*, and that of the *predominance of the flexors over the extensors*. On these questions we have already given our opinion (see p. 72).

Some important modifications are to be observed in the movements made in walking, according as they take place on level ground, or in going up and down a staircase, for instance; and these have been carefully analyzed by Marey ("Journal de l'Anatomie," 1873). We cannot pursue the subject further here, but will only give the essential features of running, as mentioned by this physiologist. In running there is no double support, but, on the contrary, a *time of suspension*, during which the body remains for a moment lifted above the ground, one foot having just left it, and the other not having yet touched it. The length of this time of suspension appears absolutely to vary very little; but if it be compared with the length of a step in running, we find that the relative value of the suspension increases with the speed of the running, because, as this increases, the length of time during which the foot remains on the ground is diminished. What is most remarkable, however, is the means by which, according to Marey, this interval of suspension is produced: we might at first suppose it to be the effect of a sort of leap, by which the body is thrown upwards,

[1] Duchenne (de Boulogne), "Physiologie des Mouvements." Paris, 1867, p. 386.

so as to describe a curve in the air, in the midst of which it is at its maximum of distance from the ground. This is not the case: the time of suspension occurs when the body is at the least distance from the ground, and is caused, not by the body being raised in the air, but by the *legs being withdrawn from the ground, during their flexion* (Marey).

PART FOURTH.

THE BLOOD AND ITS CIRCULATION.

The Blood.

The blood is a liquid which, circulating in the body from the periphery to the centre and from the centre to the periphery, diffuses throughout the system the elements absorbed by certain globules on the surface, and draws the waste parts of the system in general towards other globules on the surface, whose function it is to cast them off.[1] In

[1] It is difficult to give an exact definition of the blood. Physiologists consider it as an internal medium. "The name of medium is given to those conditions which surround a living being, and supply it with all that is needful to develop, nourish, and exhibit the life by which it is animated. . . . We must distinguish between the cosmical mediums (air, water, food, temperature, light, electricity) and the internal mediums: the former surround the individual in his perfect state; the latter belong directly to the anatomical elements of which he is composed." (Cl. Bernard, "Propriétés des Tissus Vivants.") But this general definition errs by being too general; it is easy to see that in this way all the tissues play the part of medium in reference to each other. It is better, therefore, to consider the blood as a *tissue*, as is done by most histologists in these days (Frey, Rouget), and to define it as a cellular tissue consisting of an *intercellular fluid substance*. It enters thus into one of the four great classes of tissues:—

1. Cellular tissue, with little or no intercellular substance, epitheliums and their derivatives (nails, hair, enamel, crystalline substance).

2. Cellular tissues, whose substance is fundamentally liquid (blood, lymph, chyle).

3. Cellular tissues, with abundant fundamental substance, such as mucus, hyaline, or fibrous (cartilage and all collagenous or connective tissues).

4. Tissue formed by globules, giving rise by their juxtaposition to different kinds of tubes or fibres (muscles, nerves, vessels, etc.).

this system of constant interchange it is impossible that a perfect balance should always be maintained. The blood has, consequently, no fixed normal and typical composition. We may even, in any given movement, distinguish several different kinds of blood, especially *arterial* and *venous* blood. Any analysis of the blood can therefore be considered only as approximative.

Quantity of the Blood. — It seems, at first, easy to decide on the quantity of blood contained in the body, but this also presents great practical difficulties. It is now generally admitted that the human system contains at least from five to six *litres* of blood. In order to measure this fluid mass, the attempt has been made to *bleed an animal white* (Herbst, Haidenhain); but a certain quantity of blood, which it is impossible to measure, will always remain in the vessels.

A complete injection of the vascular system, for the purpose of measuring its capacity, has been found equally unsatisfactory. A simpler, and at the same time more ingenious, method is that employed by Valentin. It consists *in calculating the quantity of blood by means of the dilution which it undergoes after the injection of a definite quantity of water*, the proportion of solid and liquid which it contained at first being known. Let us suppose, for instance, that the blood of an animal contains, at a given moment, four parts of liquid to one of solid, this proportion having been previously settled by analyzing the blood obtained by blood-letting. We then introduce into the vascular system a quantity of water equal to that of the blood which has been withdrawn, and then bleed the animal again, by doing which we naturally obtain a bloody liquid, more diluted than the first. If, for example, the first bleeding produced ten grammes, and, after the injection of ten grammes of water, the second bleeding produces blood containing twice as much water, it is easy, by a simple computation, to calculate the quantity of blood which the animal contained at first.

There are great objections to this method also, on account of the rapid change which takes place in the blood, and in the tissues that it bathes, even in the short interval between the two bleedings: the blood has, in fact, a tendency to return immediately after bleeding to its original condition, by borrowing this fluid substance from the surrounding tissues.

A still better method is that of *washing*, as employed by

Welcker. The head of an animal is cut off; all the blood which flows is collected, and its coloring power measured. The body is then cut in pieces, and, being thoroughly washed, all the blood is withdrawn. By comparing the coloring power of the bloody water thus obtained with that of the blood which was first extracted, it is easy to calculate the proportion of blood contained in the water, and to compute the quantity in the whole body. But there are objections to this method also, among which we need only mention that by washing we obtain not only the blood, but also the coloring matter of the muscles, of the marrow, of the spongy bones, of the spleen, etc.; these all being derived from that of the blood, and included in this liquid, would give it more than its proper value.

It is, however, generally agreed, as the result of experiments made in this way, that the total weight of the blood is at least one-thirteenth part of the total weight of the body, which would give for man five kilogrammes of blood, his mean weight being sixty-five kilogrammes.

The quantity of blood varies also according to circumstances: the state of fasting or digestion has the greatest effect in influencing the quantity, and the difference in these states even may be twofold. This has been directly proved by Cl. Bernard. He killed two dogs, one of which was fasting, and the other in the midst of the process of digestion. He proves it indirectly by showing that, to kill an animal in which digestion is going on, a dose of poison is required (strychnine, for instance) double that which would suffice to kill the same animal while fasting. It is true we must remember that in the former case, not only the system in general is glutted with liquids, but the anatomical elements themselves are saturated, and thus much less fitted for the absorption of poison. Collard de Martigny mentions a still more significant fact, which is this: in order to kill a rabbit in its ordinary state by bleeding, thirty grammes of blood must be taken from it; but, after a three days' inanition, the taking of seven grammes will produce the same result. We can easily see how important this fact is to the physician, in regard to bleeding a patient at the beginning of an illness, or after several days' restricted diet.

Composition of the Blood. — If we examine the blood from an anatomical point of view (as a tissue), we find that it is composed of two distinct parts: the *cruor*, which comprehends the solid part, the *globules;* and the *liquor*, which

comprehends all the liquid part in the physiological system. These two parts are in equal quantities, and we may thus define the blood as a certain *mass of cruor*, *floating in a quantity of liquor* of equal bulk.

Yet this proportion may vary, particularly in the cases already mentioned. During the process of absorption the mass of blood may be doubled; it is the liquor especially which then increases, and this increase is due to the large quantity of lymph which is poured into the circulating current. (Colin collected from a cow, by means of a fistula in the thoracic duct, as much as ninety-five litres of lymph in twenty-four hours.) After copious bleeding also, the blood has a tendency to recover its former bulk by borrowing fluid constituents from the adjacent tissues; the quantity of liquor will then be increased, the process being much slower in regard to the cruor. We know, too, that death generally ensues when half the blood has been drained away by hemorrhage, or rather, to speak correctly, when half the *cruor* has been withdrawn, the importance of which fact is evident in the case of successive bleedings; because the liquid part of the blood, and not the globules, has had time to be re-formed.

Cruor. — This is the solid part of the blood, and is formed entirely of globules, floating in liquid: the blood globules are of two kinds, *red* and *white*.

a. The *white globules of the blood*, better named *colorless globules* (Leucocytes, Robin), are a little larger than the red (from eight to nine thousandths of a millimetre in diameter), but much less numerous (there is, in general, one white to three hundred red globules); they are spherical in shape, and similar in every respect to the *lymph globules* which are found in the lymphatic glands: they originate, in fact, in these glands, and are subsequently detached from them, and drawn by the lymph into the thoracic duct, whence they spread, with the lymph, throughout the blood. These globules are round, having nuclei, and a slightly granular surface (Fig. 31). When examined in the liquor of the blood, with a magnifying power of from 200 to 300 diam., they seem to have a granular appearance and are irregular in shape, their color being a peculiar silvery white. Under these circumstances it is impossible to distinguish any other details of their structure; but, on the addition of water, we find that these elements increase in size, their outline becomes smooth, and a nucleus appears, sometimes double or multiple; the addition of acetic acid renders these features still more dis-

tinct, and sometimes divides the nucleus in several parts, or makes two or three nuclei appear at once in one globule (Fig. 31, B, *f*, *h*, *i*, *k*). Their purpose probably is to form the red globules, and we find, between these two kinds of globules some intermediate elements in respect to color and form. Under certain circumstances, and particularly in diseases of the liver, of the spleen, and of the lymphatic glands, these white globules increase in number until they form one-third or one-half of the globular portion of the blood, which then appears of a lighter color (whence the name of *leucemie* or leucocythemia). This accumulation of white globules appears to arise from some obstacle to their transformation into the red globules, or from their being produced in greater numbers by the spleen (splenetic leucocythemia), or by the lymphatic glands (lymphatic leucocythemia). But even in the physiological condition we find considerable variation in the numerical proportion of the white globules to the red: thus the former diminish under the influence of *abstinence*, and in the case of persons advanced in years; on the other hand, they increase after eating, after hemorrhage, in children, and in women during pregnancy; this increase, especially that after eating, constitutes what is called *physiological leucocytosis*. The white globules are, finally, more abundant in certain parts of the vascular system, such as the veins of the liver and of the spleen; and this is an important fact in the study of the physiology of these organs.

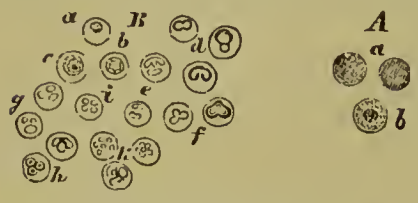


Fig. 31.—White globules of the blood (*Leucocytes*; Robin).*

b. The *red globules* (*hematies*, Gruithuisen, Robin), form the principal part of the cruor (three hundred red to one white). It has been calculated that a litre of blood contains five billions of these, which makes their entire number twenty-five billions. The red globule is thus the most largely diffused of the elements of the system; and, since nearly half the blood is composed of it, it forms the principal organ of the whole body. The process most commonly employed to determine the number of globules in any given quantity of blood is that invented by Vierordt, and improved by Potain,

* A, Fresh white globules. *a*, White globule in its natural fluid. *b*, White globule in water. B, White globules treated by acetic acid. *a*, *c*, Non-nucleated white globule. *b*, Division of the nucleus. *d*, Division (more advanced) of the nucleus; *f*, *h*, *i*, *k*, still more advanced. (Virchow, "Pathologie Cellulaire.")

and more recently by M. Malassez. It consists in diluting with a certain quantity of distilled water, collecting a portion of this mixture in a capillary tube, and deciding, by the aid of a graduated micrometer, or simply by that of the microscope, what is the quantity contained in a portion of the tube.

The *red globules*, or, properly, *blood globules*, are small disks, excavated on both surfaces, and thicker at the edges (Fig. 32); their diameter is $\frac{1}{150}$ of a millimetre, and their thickness is $\frac{1}{600}$.

Considered histologically, the red globules are small masses of protoplasm, combined with certain chemical compositions (see, farther on, *globuline*, *hematine*, etc.); seen in section, these elements appear in the form of a biscuit, narrow in the middle, and widening at the two extremities (Fig. 32, *c*). In front, they appear as disks of a yellowish color, darker at the edges, more transparent towards the centre (Fig. 32, *a*). There are no distinct nuclei or envelope, but a very thin limiting layer, which seems to indicate the presence of an enveloping membrane, or, at least, of a sort of girdle, more condensed than the globules, and having a different composition. The absence of membrane has been thought to be demonstrated by the deformities which these globules undergo when subjected to a temperature of from 40° to 45° (Ranvier), or to the action of carbonate of potash (Dujardin). Under these circumstances they become flatter, and change their shape into that of a number of caps or cups, whose edges have been recently and regularly united to each other. We observe the same phenomena, however, under like circumstances, in the bodies of the *infusoria* (Rouget), which certainly have a covering, or, at least, a cortical layer (*hautschicht* of the Germans). Finally, by the action of picric or chromic acid, we discover a distinct membrane; this is still more visible in the batrachians, in which, under the influence of hibernation, colorless vacuoles, or fragments of the coloring matter, radiating like the spokes of a wheel, are formed in the blood globules (Rouget).

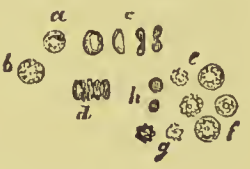


Fig 32.
Blood globules of an adult man.*

* *a*, Ordinary red globule, having the form of a disk. *b*, White globule. *c*, Red globules, seen from the side, being placed upon their edge. *d*, Red globules, piled one upon the other, like coins. *e*, Red globules, with shrunken edges, a part of the contents of which has been lost by exosmosis, whence their shrunken or crenated appearance. *f*, Red globules (the edges being uneven, and the surface exhibiting a swelling resembling a nucleus); *g*, still more shrivelled; *h*, final degree of crenation. 280 diam. (Virchow.)

The red globules change very easily: the slightest evaporation, the slightest concentration of the liquid in which they float, gives them, by exosmosis, a shrivelled form, indented or crenated (Fig. 32) at the edges, and thus, when seen in front, they present a false impression of an apparent nucleus (Fig. 32, *f*).

The form, the size, and even the structure of the red globules is not the same in different animals, or even in the same animal at different stages of development. The *globules of the human fœtus* are distinguished from those of the adult by the existence of a nucleus, and it is only towards the second half of the intra-uterine existence that they lose this feature. The blood globules of the adult mammifera are similar in form to those of man, but differ in size: those of the guinea-pig, of the goat, of the sheep, of the horse, and of the rabbit are smaller; those of the dog, about equal in size; those of the elephant, much larger. The camel and llama, alone among the mammifera, have globules elliptical in shape, and always without nucleus. In birds the globules are larger than in the mammifera, elliptical and biconvex, and present some traces of a nucleus. The globules of reptiles and of the amphibious animals (Fig. 33) are large, elliptical, and biconvex, with a visible nucleus, as is the case generally with fishes. The following figures will be sufficient to give an idea of the differences in size: in man the red globules measure $\frac{1}{150}$ of a millimetre, and in the proteus $\frac{1}{12}$.

The presence of colored globules in the blood is usually considered a distinguishing feature of vertebrate animals. Rouget has, however, long since pointed out the existence of similar elements in the invertebrate: in this case they are generally without any covering, granulated, and supplied with a coloring matter (hematine, see farther on), which, instead of being uniformly diffused, is present in small distinct quantities. The globules of the sipunculus, however, are composed of a thick, elastic envelope, with a double outline, enclosing a pinkish, homogeneous substance, which is very refrangent.

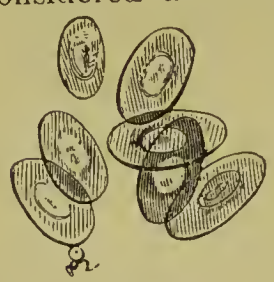


Fig. 33.—Globules of a frog's blood (Donné, "Atlas du Cours de Microscopie," Fig. 2).

In a physiological point of view the red globules are remarkable for their elasticity: they are *slightly* and *perfectly elastic;* they change their shape on the slightest pressure, but return easily to their original form. In examining the

circulation of the blood with a microscope (in the mesentery of the frog, for instance), we sometimes see the globules bend in two, or mount, as if on horseback, the spur thrown out by the bifurcation of a vessel. What is still more remarkable, they may, under certain circumstances, *alter their shape and size*, by a sort of *contractility* which is shown particularly when they are subjected to the influence of oxygen gas or of carbonic acid; the result of this change of form is a change of color. When the globule is *flattened* and *hollowed out* by the influence of oxygen, it appears brighter and redder (arterial blood); when it is *gathered*, as it were, *into a ball*, under the influence of carbonic acid, it becomes darker (dark color of the venous blood).

In a chemical point of view we notice the interesting facts that the red globules contain, as mineral substances, different salts from those of the liquor; that is to say, principally phosphates and salts of potash, while the liquor contains principally carbonates and salts of soda. We have already mentioned, as one of the general properties of the living globule (see part first, p. 7), its power of maintaining the original composition, in spite of the laws of osmosis and of diffusion. From the fact of these ingredients being found in the blood globule we may infer that salts of potash would be useful, instead of salts of soda, when our object is to restore this particular element of the blood (in aglobulia, a disease where the number of globules is diminished).

Water in the blood globule is contained in the proportion of two-thirds, a proportion inferior to that found in the globular elements generally (four-fifths). The most noticeable element

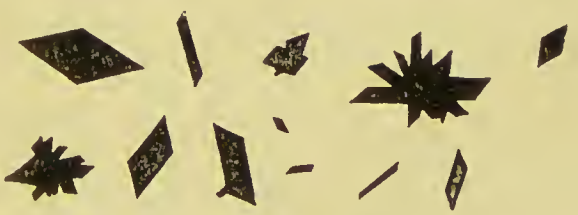


Fig. 34. — Crystals of hæmin.*

of the blood globule is an organic substance of the nature of albumen, which possesses the property of crystallization. It is called *hemoglobuline*, and is composed of *globuline* (a composition resembling *casein* rather than albumen) and of

* Obtained from the blood artificially, by the action of cooking salt and acetic acid (chloride of hematine). 300 diam. (Virchow.)

hematosine (a *proteine* substance, containing the coloring matter of the globule). By injuring or destroying the globules we obtain first a solution of a bright red, which shortly deposits crystals of different forms, varying in the case of different animals. These crystals are red, generally irregular in shape, and easily destroyed; of this class are *hemoglobuline* or *hematocrystalline*. Under the influence of different reagents this substance develops new forms, such as *hemine* and *hematoidine*, which crystallize into more regular forms and with darker colors (Fig. 34, *hemine crystals*). Hematosine contains 7 per cent of iron, and as there are about 100 grammes of hematosine in the entire mass of the blood, the quantity of iron contained in the body would appear to be about 7 or 8 grammes.

Hemoglobuline becomes crystallized sometimes spontaneously, but more particularly when under the influence of certain reactions or of certain physical actions, such as repeated freezing, followed by melting. In man it is then precipitated under the form of prismatic crystals. In the mouse and the guinea-pig the crystals are tetraedic, and hexagonal, also, in the case of the squirrel.

Hematine, on the contrary (or hematosine), which is the coloring matter of the blood, properly so called (*hemoglobuline*, without the *globuline*), forms quite spontaneously in effusions of blood in the tissues, and in blood kept for a long time in a vessel: it is always amorphous, and appears as granulations of a deep-red color.

By combining hematine with an acid, hydrochloric acid, for instance, we obtain a new body, hemine (or chlorate of hematine (Fig. 34), the crystals of which appear in the shape of rhomboid plates, flattened at the corners, and of a deep brown color. The crystals thus obtained are found only in the blood.

Hematoidine, finally, is derived from *hematine*, and is produced spontaneously in the system, particularly in old hemorrhagic spots, and generally in all effusions of blood.

This substance, which appears in the form of small rhomboid and oblique crystals, is identical with the coloring matter of the bile. Chemically considered, hematoidine is not identical with hematine; the difference is one part less of iron and one more of water.

These coloring matters of the blood, particularly the hemato-crystalline, have been, during the last few years, the object of very interesting researches, by means of their *spectral*

analysis. Hoppe Seyler (1862) and Valentin, in Germany; Stokes and Sorby, in England; Bert, Claude Bernard, Benoît,[1] and Fumouze,[2] in France, have, by applying to the study of the blood the means of analysis discovered by Kirchoff and Bunsen, shown that when a large solution of arterial blood is examined through a prism (spectroscope) by the light of the sun or of a lamp, we find, instead of the

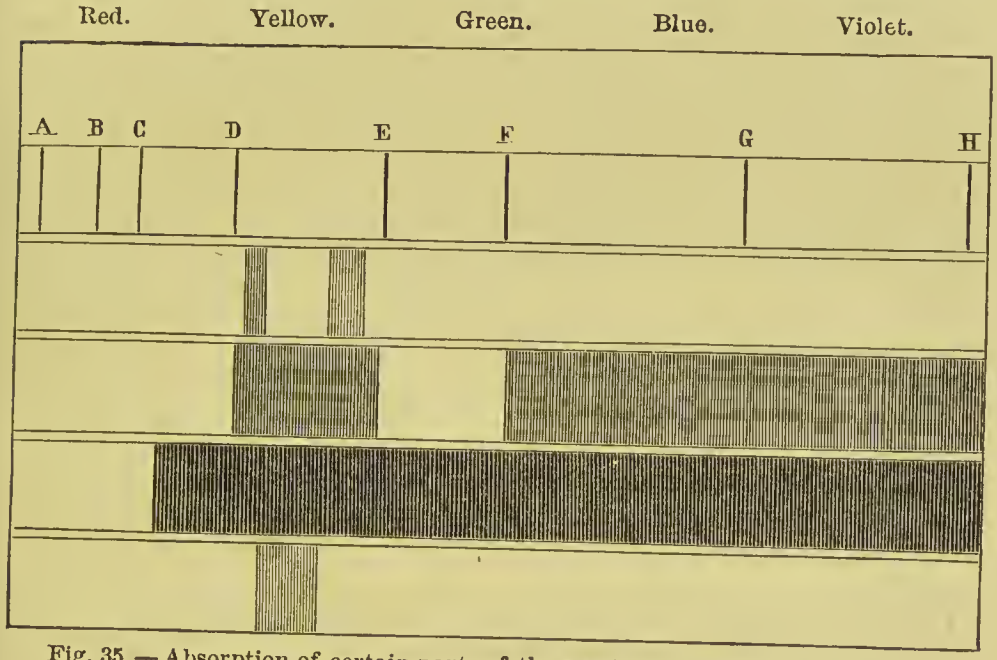


Fig. 35. — Absorption of certain parts of the spectrum by solutions of blood.*

ordinary luminous spectrum, one crossed by broad dark bands (placed as in Fig. 35); this is called the *absorption spectrum of the blood:* it is essentially characterized by two dark bands in the yellow and green, and also by the almost entire extinction of the most refrangible rays, beginning at the blue or the indigo (Fig. 35, C).

It is remarkable that the venous blood, and that which has

[1] R. Benoit, "Études Spectroscopiques sur le Sang." Thèse, Montpelier, 1869.

[2] Fumouze, "Les Spectres d'Absorption du Sang." Paris, 1871, in 4to.

* A, Fraünhofer lines. B, Oxygenated arterial blood (two bands of absorption between the lines D and E of Fraünhofer, that is, in the yellow of the spectrum). C, Arterial blood in a more concentrated state of solution (absorption of all the rays beginning at F, that is, the blue). D, Solution still more concentrated. E, Venous blood, reduced blood; absorption band near the line D of Fraunhofer (that is, in the yellow). (Paul Bert.)

lost its oxygen, as well as solutions of hemoglobuline which have been deoxidized by any reducing agent, present a different spectrum: the interval which separates the two bands is darkened, or, in other words, the two black bands fuse into one (*reduction band of Stokes*) (Fig. 35, E). At the same time the shading which covers the most refrangible part is withdrawn towards the violet, so that there is more transparency to the blue rays.

There is thus a spectrum of oxygenated blood and of deoxidized blood, of oxygenated hemoglobuline and of *reduced* hemoglobuline.

Claude Bernard and Hoppe Seyler demonstrated, at about the same time, that oxide of carbon drives the oxygen from the blood and takes its place, entering into combination with hemoglobuline. This combination gives a spectrum (spectrum of oxycarbonated blood, very similar to that of the oxygenated blood, with the exception of the two black bands being slightly displaced towards the right. The principal feature in this spectrum is that the action of reducing elements produces no change in it; in other words, the spectrum of oxycarbonated hemoglobuline does not furnish, like that of oxygenated hemoglobuline, Stokes's *band of reduction.* The importance of these discoveries and of their application is evident in the case, for instance, of a person suffocated either by the fumes of charcoal or the oxide of carbon. It is also important to notice that these distinguishing bands can be obtained by washing with water old blood-stains upon iron, wood, linen, etc., even where the blood is already decomposed and putrid. Valentin has proved satisfactorily the presence of blood upon a board taken from a dissecting table, which had lain unused in a damp place for three years, and also upon a rusty butcher's hook, which had been long thrown aside. Numerous attempts have been made in vain (Kitter) to discover any coloring matter, of which the spectrum could possibly be mistaken for that of the blood, or which could, by means of the agents of reduction, show any thing analogous to the *band* of Stokes.

This method of research is beyond almost every thing that could be desired on the score of minuteness; for Valentin has discovered indisputable traces of the blood spectrum in a solution containing only seven-thousandths of blood in a thin layer of fifteen millimètres.

By successive study of the spectrum of oxygenated and deoxygenated blood, of oxygenated and reduced hemoglob-

uline, which spectra can be produced by alternately taking away and restoring the oxygen of the solution of blood, we bring a new element to the explanation of the difference of color in arterial and venous blood. This difference is not due only to changes in form in the globules, for these changes in color, which correspond with the differences in the spectrum of arterial and venous blood, are, like these, the result of alternations of oxidation and of reduction of the hemoglobuline, so that the arterial and venous blood represent the two states of oxidation and reduction of the coloring matter of the blood.

The physiological function of the red globules consists entirely in the absorption of oxygen which they then impart to the tissues. They are the receptacles, the condensing apparatus of this gas, similar, so to speak, to coal and to the sponge of platina. In traversing the pulmonary capillaries they borrow the oxygen from the outer air, and then carry it to the different parts of the system, especially to those which consume this gas in large quantities, that is, the nerve globules, the nerves, and the muscles. These elements give back, in exchange for the oxygen which they receive, a nearly equal quantity (see respiration) of carbonic acid, a small part of which remains in the blood globules, the larger part being dissolved in the liquid, or liquor of the blood.

The functions of the blood globules are thus principally mechanical, on account of the movements to which they are subjected, and of their connection with the gaseous interchange. We may also say that *the principal object of these functions is to excite or support the nervous system*, as the nerves can exist only where the blood globules are properly constituted, and contain the necessary quantity of oxygen gas. Thus no animal can lose, unharmed, more than one-fifth of its blood, or of the mass of its cruor. If it does, it succumbs, with symptoms which resemble those attending a nervous fever, such as prostration, loss of sensibility, buzzing in the ears, deafness, convulsive movements, dyspnœa, and death. The transfusion of fresh blood, defibrinated (in one word, the *transfusion of globules*), will remove these symptoms, and bring back life, if done in time; the transfusion of the liquor alone will not suffice.

The transfusion of blood consists, essentially, in bringing a new supply of blood globules. This operation responds neither to the exaggerated hopes of the restoration of youth, of the cure of madness, etc., nor to the unreasonable fears

which it excited at its first discovery in the seventeenth century, whence the practice of it was forbidden by the Parliament of 1668. (Lower, Denis.) To-day, we count by hundreds cases of hemorrhage, where the invalid has been recalled to life by the transfusion of blood, especially in the case of metrorrhagia. In order to produce the desired effect, the blood globules must be taken from an animal of the same kind. Any others would be no more capable of restoring life than the spermatozoids of one would be to propagate the ovula of the other. A very small quantity of blood is sufficient to produce this vital change, and to enable the patient to regain the usual quantity, by the process of nutrition. Transfusion has also been applied in cases of poisoning, and is a very proper agent in the case, for instance, of poisoning by oxide of carbon, which causes paralysis of the red globules; it has been found successful (Rouget), the useless globules being replaced by new ones and so capable of their nutritive and respiratory functions. In other kinds of poisoning and in the uremia, this method does not succeed as well.

The red globules are thus what may be called *the organ of the blood.* When they increase disproportionately, a kind of *plethora* ensues, circulation is impeded, and congestion is likely to follow. Something analogous to this takes place in the cholera, but by an entirely different method; there the immense waste of liquids by the intestines renders the blood extremely thick; the globules uniting, make the blood *gluey.* In all chronic, and in most acute diseases, where a strict regimen has been long observed, a sensible diminution takes place in the organ of the blood (see p. 112), corresponding with the length of the malady. It attains its height in anæmia and in chlorosis, and cases of chlorosis have been known in which the cruor formed only a quarter of the mass of the blood; what is called hydræmia (a corresponding increase in the watery part of the blood being understood) then takes place.

In their own life, the blood globules exhibit different phases of existence; they undergo changes; there are young globules, and old globules. The former are, in the adult, produced by the transformation of the colorless (the white) globules of the lymph.

The transformation of white globules into red, which some histologists consider doubtful is, nevertheless, shown us by many proofs. The first which we shall mention is the direct one furnished by Recklinghausen, and, more recently, by

Kölliker, who have seen the transformation of white globules into red produced even outside the organism, in blood kept at the temperature of the living body, in contact with a moist atmosphere. On the other hand the study of the blood in the animal series shows all the transitions between the two kinds of globules. Rouget has shown what they are in the case of the invertebrate animals, the sipunculi. In the inferior vertebrate animals, particularly the mole (Kölliker, Rouget), we observe the transformation of the lymphatic corpuscles into colored globules, provided with a nucleus, the coloring matter being first deposited under the form of granulations, and then spreading uniformly throughout the globules. Rouget has observed the same transformation in the embryo of rabbits; here the nucleus diminishes, and at length disappears, while the coloring matter is deposited first in patches, and afterwards generally diffused. Finally, there have been found in the thoracic duct, and even in the pulmonary veins (Kölliker) young red globules in an intermediate stage between the white globules and the perfect red. As to the indirect proofs of this transformation, it will be sufficient to remark that the lymphatic glands and the spleen are continually pouring white globules into the current of the blood. Now, as we do not find that their number increases in the blood, and know of no proof of their being destroyed, we are forced to conclude that they disappear by being changed into red globules. Finally, these red globules must have had an origin, and been derived from a pre-existing cell, for they exhibit globular forms which are already old, the loss of the nucleus and the presence of coloring matter being taken into account; if we accept the theory of the *genesis* for the production of the white globules, which are elements in an early stage, we cannot do the same in the case of the red, which are old forms of elements: the early stage of the red globules can be represented only by the white.

In their temporary condition the red globules themselves exhaust a part of the oxygen with which they are charged, the presence of this oxygen being necessary to their vitality and to their form. In making experiments, whenever it is desired to filter blood, care must be taken to introduce into the liquid a current of oxygen, which prevents the solution of the globules in the liquor. When destroyed in the system, the globules leave what are evidently the products of their decomposition. It is true that there are hardly any

elements in the blood which can be considered as the waste part of the globules, but there are organs in which it is evident that they are decomposed. If we compare the blood which enters the spleen with that which leaves it, we observe a diminution of half the cruor, whence we must conclude that the globules disappear in this organ. The examination of the spleen, too, reveals the presence of many elements which have the appearance of old blood globules. The blood of the portal vein resembles ordinary blood, but is more hydræmic, being impoverished by mixing with the blood of the splenic vein, which has been already deteriorated in the spleen. In the hepatic veins we find, on the contrary, that the globules have increased in the proportion of one-half to two-thirds. Thus the liver, in opposition to the spleen, may be a sort of factory for the production of blood globules.

The *hemopoietic* function of the liver is not, however, sufficiently proved, and the numbers which lead to our belief in it may even be differently explained. These numbers show the relation of the globules to the liquid part of the blood, of the *cruor* to the *liquor ;* that is, according to Lehmann, that a thousand parts of the blood of the portal vein (in the horse) contain only 141 parts of red globules (in weight), while we find 317 to a thousand in the hepatic blood. This increase does not, however, always take place; it has been shown that, after the formation of bile, the plasma of the blood is much concentrated, so that the water in the blood coming from the liver forms $\frac{68}{100}$ of the whole of the constituent parts, while water forms $\frac{77}{100}$ of the blood in the portal vein. In a liquid so concentrated as the hepatic blood, the increase of the red globules cannot be looked upon as invariable. On the other hand, the figures given us by Lehmann represent the weight of the liquid globules; now in the typical arterial blood, the weight of the liquid globules is 500 to 1000 (half cruor and half liquor). A careful examination of the figures thus leads to the conclusion that the red globules are rather destroyed, than formed, in the liver. A direct proof is given by finding out the proportion of red to white globules in the blood of the portal veins and in that of the hepatic veins; the following is the result: one white globule to 740 red in the portal vein, and one white globule to 170 red in the hepatic veins. This difference shows either that white globules are produced in the liver, or that the red are destroyed. The former hypothesis is directly opposed to

what we know of the physiology of the liver: the latter, on the contrary, agrees perfectly with the biliary functions of this organ, the coloring matter of the bile being identical with hematoidine, one of the derivatives of the blood. It is useless to object that we find colored bile in animals whose blood is colorless (the invertebrate); for Rouget has found colored globules in many of these animals, and in others hemoglobuline, or a substance analogous to it, is found in a diffuse state, dissolved in bloody serum. This has been proved by Fumouze, by the aid of spectral analysis, even in the case of animals whose blood appears quite colorless, and we may thence conclude that the liver is one of the places in which the *old* red globules are destroyed.

Liquor. — The liquid part of the blood (*liquor* or plasma of the blood) may be considered as a solution of albumen, containing besides several salts, fats, extractive matters, and gases.

The *liquor* is a fluid comparatively loaded with albumen, containing nearly one-tenth, a proportion rarely met with in the other fluids of the system. A small part of this albumen (2 grammes to 1 litre of blood) coagulates spontaneously: this is called *fibrine.* The rest (70 to 75 grammes to a litre of blood) is albumen, properly so called, which coagulates only by the action of heat or of chemical reagents.

The fibrine is the cause of the coagulation of the blood, that is to say, of the phenomena by which, on leaving the vessels, the blood is solidified into a jelly-like mass. It is the fibrine alone which is coagulated in this case, and forms a kind of net in which the other elements of the blood, and especially the globules, are imprisoned. We do not mean by this that the fibrine becomes a fibre, as its name would appear to indicate; it forms, rather, a sort of spongy mass, containing in its meshes all the other parts of the blood. As coagulation proceeds the liquid part takes the form of *serum*, a limpid or slightly opaline liquid, which contains albumen and the various salts of the liquor; the coagulated mass which floats forms the *clot.* The clot must not be confounded with the *cruor;* it is the *fibrine absorbing the cruor:* neither is the *serum* synonymous with the *liquor*, it being *the liquor without the fibrine.*

It is not ascertained what circumstances are most favorable to the coagulation of the blood. It is hindered by cold, and accelerated by contact with the air. Beating, which is employed to defibrinate the blood, acts only by rendering

the contact between the air and the fibrine closer and more general. By this means the fibrine coagulates rapidly, and hangs in shreds from the instrument employed. The globules appear to have some share in this phenomenon, and seem to aid in solidifying the fibrine. We know that coagulation is retarded by the mixture with the blood of such substances as sugar, salt, or any alkali. In this case a certain number of the globules do not become enclosed in the fibrine, but color the serum red, while the clot is paler, or even quite white, in its upper coats (*couenne*): these fibrous buffy coats are also found in some pathological conditions, in diseases of the lungs, for instance, and here we find the fibrous sponge enclosing globules covered with a layer of pure fibrine, which has a whitish tint, or is coated, thus containing the white globules (which, by their lightness, have a tendency to rise to the surface) (Fig. 36). This phenomenon may have two different causes, independently of an excess of fibrine: either the blood globules (the red) have become specifically heavier, or coagulation is slower. In the former case they are not at the same level in the liquid as the fibrine which floats and coagulates apart: in the latter they have time to sink, while the fibrine coagulates slowly. In horses coagulated blood shows always a buffy coat.

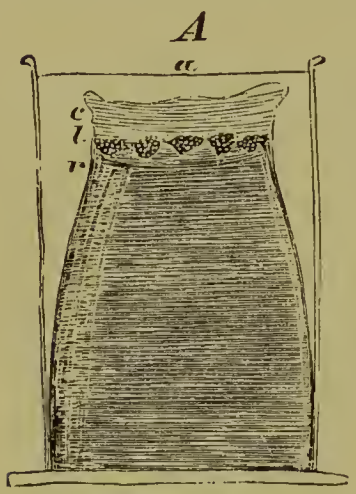


Fig. 36. — Coagulated blood with a buffy coat.*

The fibrine was formerly looked upon as a most important part of the system: it was considered, on the one hand, to be the nutritive substance, *par excellence*, perfected albumen; on the other, to be a part of the organization, on account of the apparently fibrous structure which it exhibits when coagulated. At present it is admitted that this is a mistake: fibrine is rarely found in the most nutritive substances, and the quantity in the blood does not increase with the increased vigor of the subject; on the contrary, it is found to accumulate after fasting, after a fatiguing walk, in diseases where there is great emaciation, in cases of want of nutrition, in chlorosis, etc. It is more

* *a*, Level of the liquor sanguinis. *c*, Buffy coat, in the form of a cup. *l*, Granular layer, with granular collection of white globules. *r*, Clot, with red globules. (Cruor and red clot.) (Virchow, "Pathologie Cellulaire.")

abundant in adults than in children. When an animal is bled, and thus deprived of a large quantity of fibrine, it is easily ascertained that the fibrine is reproduced shortly afterwards. Thus it does not come from outside: it is formed in the organism, and examination of the circumstances under which it increases proves that it constitutes an organic waste which gives rise by its decomposition to the urea and to uric acid: these elements, in fact, appear in the urine after inflammations in which there has been an excess of fibrine in the blood.

The experiments of Brown-Séquard show that in the physiological condition fibrine is produced, above all, in the muscles, and that the blood which comes from a muscle is richer in fibrine the more the muscle has been exercised, as, for instance, when under the influence of galvanism. Fibrine is, then, an excrementitious form of the products of nutrition of the tissues, being found in greater abundance when the tissue has received more nutrition. It is difficult to decide where the fibrine disappears or is destroyed. It has been supposed that there is no fibrine in the blood which comes from the liver. This is, however, an error. The blood of the liver is as rich in fibrine as that of the spleen or the muscles, and it only appears to be without it when, in dissection, the bile is allowed to mix with the blood drawn from this organ (Vulpian). Too severe labor, or organic combustion, always produces an excess of fibrine in the blood; in all inflammation there is *hyperinosis;* this hyperinosis is entirely secondary, and not at all the cause of the state of fever or inflammation. In effusions no fibrine is found, unless the neighboring tissues are in a state of inflammation capable of giving rise to an excess of this organic waste: thus, the liquid of hydrothorax contains no fibrine; that of pleurisy, on the contrary, a great deal, etc.

The liquid which remains after the coagulation of the fibrine is called the *serum.* It contains, as we have already said, a large proportion of albumen (between 70 and 75 grammes to 1000 parts) which does not coagulate spontaneously. The serum finds its way easily out of the vessels either by osmosis, or more frequently by simple transudation, because in cases of stoppage of the blood by a ligature or by compression it has been observed that the albumen abundantly transudes. It is generally supposed that the object of the normal transudation of the albumen is the nutrition of the tissues; this, however, is by no means certain; and,

indeed, we find, in addition to the albumen, a series of albuminoid substances called *peptones*, not coagulable by heat, and appearing particularly well adapted for transformation easily and readily into the form of tissue. It is more likely that the principal use of ordinary albumen is to prevent the adhesion of the blood to the coats of the vessels.

The serum contains various *fatty matters*. In some cases it is difficult to account for the presence of these fats. Thus, in the case of persons who are habitual inebriates, drops of fat are sometimes found floating in the blood; after an abundant meal, also, an accumulation of fatty globules is found in the blood, which, however, soon disappear. A fatty substance, also, which is not capable of saponification, is generally found in the serum (cholesterine); this is admitted to be an excrementitious product (to be rejected by the liver). In addition to these fats are found the fatty elements (margarine, oleine; margarates and oleates of soda) and fat acids peculiar to each animal, and which may be removed by means of sulphuric acid. These volatile fat acids, when thus removed, emit a peculiar odor, by means of which the blood of man can be distinguished from that of other animals, and it has even been asserted, the blood of a man from that of a woman. The sum total of fatty matters contained on an average in the blood is from 2 or 3 grammes in a litre.

There are, besides, found in the *liquor* some compositions which it is difficult to classify, known by the name of *extractive matters*. Among these complex substances we will mention the *lactic acid* and the *lactates*, which are formed, no doubt, principally during the process of digestion; also, the *pneumic acid*, whose existence is still doubtful, but which is probably due to a reaction in the lung, which releases the carbonic acid from the venous blood; also, the *urea* and *uric acid*, excrementitious products destined to be thrown off, whose retention in the blood is highly dangerous; also, the *creatine* and *creatinine*.

We must also mention here the *coloring matters* which, no doubt, originate in the globules, reappearing in some secretions, especially in the bile; and, finally, those compositions, belonging to the class of *sugars*, which arise partly from the ingested substances, and partly also, perhaps, from the transformations which take place in the different tissues, glands, and particularly in the liver; their function is, perhaps, more essentially glycogenic (see "digestion; functions of the liver").

The *salts* contained in the serum (and consequently in the *liquor*) are not identical with those which we have described as found in the globules. The salts contained in the blood is about 8 or 10 in 1000 parts, the principal portion being of an alkaline character. Soda, especially in the form of carbonate, is the basis of most of the salts in the *liquor*. The serum is extremely alkaline, and the necessity of this reaction is plain, if we remember all the reductions to be made in this liquid. There are, besides, few metals whose presence has not been suspected in the blood (*liquor and cruor*); iron and manganese have been found in it, and occasionally copper, which we might, perhaps, consider a normal constituent. It is also asserted that arsenic has been discovered; lead rarely: these are, however, simply chemical curiosities. (These last-named substances exist in such minute quantities that we might leave them out of consideration. Am. ed.)

Gas of the Blood. — The blood contains not only solids and liquids, but gases also. Considered in regard to respiration the blood is really a solution of gas. 1. We have already seen that the red globule is the medium of a certain quantity of *oxygen*. A smaller proportion of the same gas is dissolved in the *liquor*. 2. The carbonic acid is contained wholly in the serum, partly in a state of solution, partly combined with the alkaline carbonates, which thus pass into the state of bi-carbonates (Emile Fernet).[1] We shall study the gases of the blood more fully when we come to the subject of respiration, and we shall thus discover that the blood is the essential vehicle of those gases, which supply the combustion of the tissues or may be the result of combustion.

The question of the albuminoid substances of the blood is one of those which have been the most studied, and yet is far from being completely elucidated. It is now proved that the fibrine is not produced in the globules, as was formerly believed, and that it does not represent a substance dissolved in the blood, either by the action of chloride of sodium or of ammonia (Richardson), though the liquefying action of these substances is undeniable. Robin and Verdeil had already demonstrated (1851) that fibrine does not pre-exist in the blood as a concrete substance, but naturally is in a liquid state, and generally only ceases to be so when taken from the system. Now, however, we go further, and recent researches, which are still incomplete, lead us to look upon it as the result of

[1] Emile Fernet, "Du Rôle des Principaux Éléments du Sang dans l'Absorption ou le Dégagement des Gaz de la Respiration." Paris, 1858, in 4to.

a decomposition, until its relation to those other albuminoid substances found with it in the *liquor* of the blood is more fully established.

We shall not speak of the theory of Béchamp and Estor, who maintain that the fibrine is formed by the union of those organic living molecules which they have termed *microzymas*. These researches have not yet been established by observed facts and experiments, which form the ordinary domain of science. Denis (of Commercy), in France, and Schmidt, in Germany, have found similar results in a series of researches which were extremely fruitful in pathological applications, and are so important that we cannot resist giving a short *résumé* of them, in order to complete the study of the *serum*.

According to Schmidt and Denis (of Commercy), the albuminous part of the blood is composed of two substances, of which one, *serine* (52 to 1000 of blood), coagulates only by the action of heat or of acids; the other, *plasmine* (25 to 1000 of blood), coagulates under the influence of chloride of sodium, and may be redissolved in from 10 to 20 parts of its weight of water. A part of the solution, however, as of the original plasmine, may separate spontaneously and coagulate; this is *concrete fibrine* (3 or 4 to 1000 parts of blood): the rest remains dissolved, but coagulates under the influence of sulphate of magnesia; this is *dissolved fibrine* (22 to 1000 parts of blood). The coagulation of the blood is thus the result of the separation of the plasmine into dissolved and concrete fibrine. The variations in the quantity of fibrine in coagulated blood are entirely owing to a decomposition which divides the plasmine more or less unequally into its two products. When we find an excess of *concrete fibrine* (8 grammes, for instance), there is a diminution of the dissolved fibrine (17 only in the example chosen), and *vice versâ*.

We can understand, in this way, all that was still obscure in physiology, as the pathology of the coagulation of the blood. Thus the blood which comes from the liver apparently contains no fibrine; but if its plasmine be precipitated by chloride of sodium, and the coagulum dissolved in from 10 to 20 parts of its weight of water, the normal quantity of concrete fibrine (2 to 4 gr.) will be precipitated, either spontaneously or by beating. The plasmine of the blood from the liver thus contains the two kinds of fibrine, but a cause, which it is still difficult to decide (see p. 127, above), has prevented their separation, and concealed the existence of the concrete fibrine, as it was formerly known. On the other hand, we recognize, as a general rule, the increased size of the clot and of fibrine in inflammations. There are some inflammations, however, in which we think we discover some diminution in the coagulable element, *hypinosis;* but here also concrete fibrine prevails over dissolved fibrine in the composition of the plasmine, and appears immediately, if a separation of the latter and formation of the clot be artificially produced (precipitation by chloride of sodium, solution in 10 times its weight of water, exposure to the air, beating,

etc.). We may thus conclude, with Germain Sée ("Pathologie Expérimentale:" *Anémies*), that, as a general rule in diseases, especially where there is anæmia, there is really neither an excess or a want of fibrine, but the plasmine is more or less perfect, that is, more or less easily divided into two elements, thus partaking of its nature in different degrees. Finally, according to Vulpian, all the albuminous parts of the blood form probably a composition, two parts of which, serine and plasmine (with its two elements) are the result of a division, as alcohol and carbonic acid are produced in the analysis of sugar. This explanation throws fresh light on the pathogeny of albuminuria, especially of that sort caused by changes in the albumen of the blood, and of albuminuria occurring after the artificial ingestion or injection of albumen, even of albumen taken previously from the blood of the animal. (Experiment of Cl. Bernard, of Stokvis, of Calmettes.)

Circulation of the Blood.

The *circulation* consists of the continued movement of the blood in a circular reservoir formed of ramified tubes (circulatory apparatus). This apparatus, looked at as a whole, is simply a series of tubes, with different functions and properties (Fig. 37). These are: 1. *The heart*, a muscular reservoir, divided into four cavities (in man, but more simple in the lower animals). At first it also forms a cylindrical tube, which during the life of the embryo becomes twisted, and is divided so as to form the auricles and the ventricles. 2. *The arteries*, a system of ramified tubes, in the shape of a tree, especially remarkable for the thickness and strength of their coats (Fig. 37, *a*). 3. *The veins*, another system ramified like that of the arteries, but

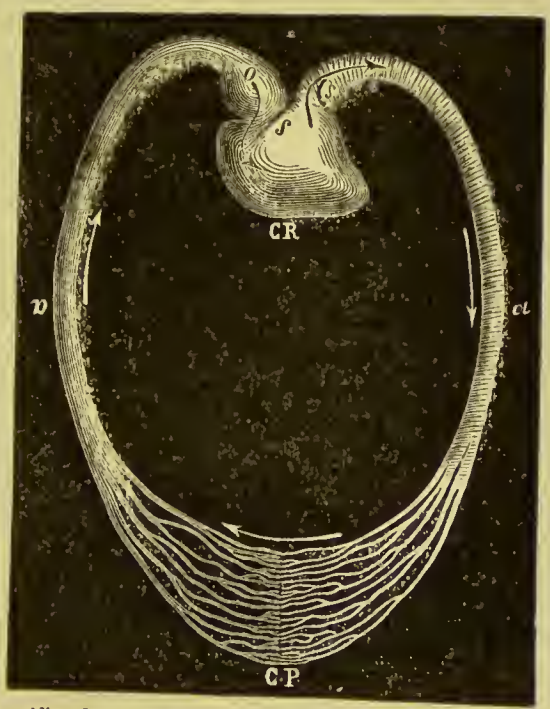


Fig. 37. — Plan of the circulating system.*

* CR, Heart, ventricle (*o*, auricle; *s*, *s*, valves). *a*, Arteries. CP, Capillaries. *p*, Veins. The arrows show the direction in which the liquid flows.

distinguished from the latter by the thinness and flaccidity of their coats (Fig. 37, *p*). 4. Between these two systems is the *capillary system* (beginning in the arteries and ending in the veins), a collection of very fine vessels, arranged like the string in a net (Fig. 37, C P), the smallest having generally the same diameter as the blood globules); their calibre is even less sometimes, but the globules being elastic can become so long and thin that they can traverse tubes much smaller than themselves.

The whole of the circulatory system may thus be divided into a central organ, *the heart*, and a number of peripheral organs, *the vessels* (arteries, capillaries, veins).

The blood circulates in a system of vessels, because at the beginning of this system (origin of the aorta) is found one of the cavities of the heart, which possesses the property of producing a strong pressure (the ventricle), while at the other extremity (vena cava) is found another cavity of the heart (the auricle), whose property it is to diminish the pressure, or at least to allow a free passage to the blood which it receives, in order to transmit this fluid to the ventricle; by this double antagonism between the two cavities of the heart the circulation is produced.

In short, the circulation of the blood is caused by the *inequality of pressure* in the different parts of the vascular circuit, and the use of the heart, taken as a whole (auricles and ventricles), is to keep up this inequality of pressure, which makes the blood pass from the arteries where the pressure is strong into the veins where it becomes gradually weaker.

The ideas entertained by the ancients as to the circulation of the blood were false and incomplete. Galen supposed the blood to be formed in the liver, and that, on leaving this organ, it spread through the lower part of the body by means of the inferior vena cava, and through the upper part by means of the superior vena cava: that, as a portion of this latter blood reached the heart, and filtered through the interventricular partition, it acquired new properties, by means of which it circulated through the arteries under the name of *vital spirits*. Galen had thus no suspicion of the existence of the *pulmonary circulation* (see farther on, p. 142).

The idea of *pulmonary circulation* was first suggested by Michel Servet, in 1553. Fabrice, of Acquapendente, first demonstrated the arrangement of the venous valves, which contradicted the theory of circulation, as conceived by Galen.

Harvey finally (1615–1628) established the theory of the circulation of the blood as we hold it at this day.

I. Of the Central Organ of the Circulation; of the Heart.

In order to comprehend the functions of the heart we must not think of it as we find it in the dead body, for there is no trace there of the muscular *elasticity*, which is one of the most important properties of a muscle, just as important as the *contractility*, and having a special purpose in that cavity of the heart called the auricle.

Auricle. — The chief function of the auricle, on account of its power of dilatation, facilitates the flow of the venous blood; it may be said *to have the same effect as blood-letting at the extremity of the venous system*, by which the pressure of the fluid is consequently diminished. During four-fifths of the time occupied by a cardiac revolution the auricle is in a state of repose, and fills with blood, or rather, allows itself to be filled, for it exercises little or no active aspiration on the venous blood (see Respiration). It resembles, at this moment, a soap-bubble, distended by air blown into it: thus it becomes the receptacle of the blood, the ante-chamber of the ventricle, a receptacle wherein a large quantity of blood accumulates; and the auricular capacity being greater than that of the ventricle, which it can immediately fill without itself becoming completely emptied.

When the auricle is full of blood it contracts suddenly, and drives the blood towards the ventricle, as it were, in the twinkling of an eye. Its contraction lasts from one-fourth to one-fifth of the total cycle. Supposing that the heart contracts sixty times in a minute, the contraction of the auricle would last only one-fourth or one-fifth of a second, the rest of the time being in a state of repose. By computing its times of activity and repose, we might say that the auricle is relaxed during eighteen hours out of the twenty-four.

The contraction of this cavity tends to throw its contents towards the ventricle, or to return them to the veins. There are no valves in the direction of the veins (Eustachian valve being excepted), or they are placed at a distance, and are consequently incapable of preventing this reflux; but the veins are full of blood, under feeble pressure, it is true, but, nevertheless, some resistance is thus offered to the return of the auricular contents. The condition of the ventricle is at

this time entirely different; it is empty, completely relaxed, and, consequently, offers no resistance whatever: the part which it now plays in regard to the auricle is the same as that previously sustained by the auricle in regard to the veins; and *the elasticity of the muscle, when in a state of repose*, allows the ventricle to be distended (see physiology of the muscle, p. 81) with as little resistance as would be offered by a soap-bubble. Thus the blood of the contracted auricle, meeting with a slight resistance from the veins, and none at all from the ventricle, is precipitated into the latter, and fills it. If the muscular tissue of the ventricle is diseased, and its elasticity diminished, a certain reflux will sometimes take place into the veins, which is one of the causes of the pathological venous pulse: this venous pulse always exists to a slight degree, but is usually scarcely perceptible.

The auricle is not, however, completely emptied, and its opposite sides do not come in contact with each other. Its rapid contraction being terminated, resumes the position of a passive organ, and allows the blood which fills the venous system to flow freely into its cavity.

Ventricle. — The ventricle is hardly full before the blood, by its contact with the walls of this cavity, occasions their contraction. The ventricular systole thus immediately succeeds the auricular systole; but the former *lasts a long time*, because the ventricle is obliged to empty its contents into a cavity which is already full of blood, and which offers some resistance to the entrance of more. By this contraction and prolonged effort the contents of the ventricle pass into the corresponding artery *without any reflux towards the auricle.*

How is this reflux towards the auricle prevented? By means of a special apparatus called the *auriculo-ventricular valves*, which really form a sort of sleeve or bag hanging from the edges of the auricle into the ventricle, and alternately approaching and withdrawing from the walls of the latter. The name "valve" shows that the rôle of this organ[1] was not at first understood. It is now shown that the *tricuspid* or *mitral valve* does not serve as a plug, but is only a movable continuation of the auricle, acted upon by certain

[1] See V. L. Kohl, "Etude Critique sur la Physiologie de l'Appareil Auriculo-ventriculaire. Thèse de Strasbourg, 1869, No. 231.

muscular powers. In fact, a large number of *papillary muscles*, having as many as 100 tendons in the right heart, and 120 in the left, are inserted in the edges and external surface of this auriculo-ventricular apparatus. When the ventricle contracts, these papillary muscles also come into play. It was formerly supposed that these muscles and the tendons belonging to them must serve to prevent the supposed valve from being too much stretched in consequence of a retrograde effort of the blood, and from being turned wrong side out in the auricular cavity. But their function is entirely different, for if the finger be introduced into the auriculo-ventricular region at the moment of the systole of the ventricle, we find that the kind of funnel which hangs from the auricle to the ventricle is continued; it even appears to

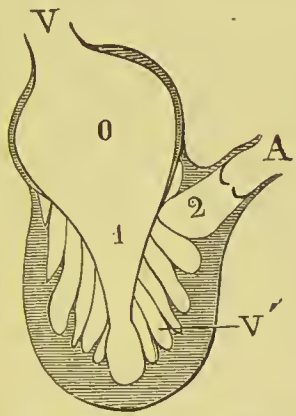


Fig. 38.—Showing the auriculo-ventricular system during the repose of the ventricle.*

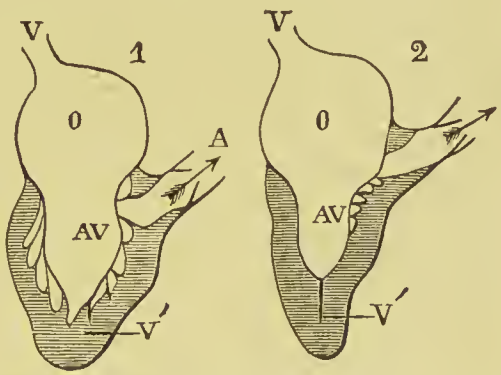


Fig. 39.—Showing the auriculo-ventricular apparatus during the contraction of the ventricle.†

lengthen itself out, and the finger, as it were, is drawn into the interior of the ventricle. In fact, the first result of the contraction of the papillary muscles is the lengthening of the auricular cone, the edges of which are afterwards brought near each other. While this hollow cone descends into the ventricle, the sides of the latter contract, and approach the cone in such a manner that the auriculo-ventricular apparatus acts as a sort of hollow piston, which penetrates the ventricle and comes into close contact with its walls, and thus the

* V, Vein. O, Auricle. V′, Coats of the ventricle, with the papillary muscles and their tendons. A, Artery. 1, Cavity of the auriculo-ventricular apparatus. 2, Infundibulum.

† 1, During the first half of the ventricular systole. 2, At the end of this systole. A V, The hollow piston formed by the auriculo-ventricular apparatus. O Auricle. V, Coats of the ventricle. A, Pulmonary artery and (arterial) aorta.

ventricle (Fig. 39) empties itself completely, the contact becoming perfect between its sides and the auricular prolongation.

The result of this mechanism, which is so simple, and yet so generally misunderstood, is that no reflux of blood into the auricle can take place: the auricle, even by means of the mechanism which we have described, exercises a sort of suction upon the venous blood, its cavity being continued so far into the ventricle. We see, also, that when the ventricular systole is complete, the lengthened tube, the hollow cone which unites the ventricle and the auricle, is full of blood, and that a slight and rapid contraction of the auricle is sufficient to drive this blood into the ventricle and fill it.

Nearly all the standard works admit, without discussion, the theory of the occlusion of the auriculo-ventricular orifices by the simple mechanism of a plug or valve, just as in the case of the arterial orifices (see farther on), but without remarking the entire difference of structure which distinguishes the auriculo-ventricular valves from the semilunar valves of the aorta and of the pulmonary artery. This theory has become, up to a certain point, the property of Chauveau and Faivre, on account of the interesting experiments which they have so often made upon horses, killed instantaneously by section of the bulb, and in which artificial respiration was kept up. "If, under these circumstances, the finger is introduced into one of the auricles, and the auriculo-ventricular orifice explored, the tricuspid valves will, at the moment that the ventricles begin to contract, be felt to straighten, appose their edges, and stretch in such a manner as to become convex, and form *concave domes* above the ventricular cavity." This method of proof does not always furnish such decided results; the finger thus introduced has given to many other observers quite different sensations. Onimus found the auriculo-ventricular orifices effaced by the contraction of the muscular fibres, which, at this level, really form a sphincter (this is the case in the heart of birds, but not of the mammalia). The papillary muscles, being now contracted, lower the valves, and these, supporting themselves against the sides of the ventricles, have the effect of driving the blood, engulfed between them and the corresponding sides, into the arterial orifices. Such is, in short, the working of the auriculo-ventricular membranes. This is the only theory which accounts for the existence and arrangement of the papillary muscles.

It was first suggested by Parchappe (1848); was chiefly developed by Burdach; afterwards by Purkinjé and Nega (1852); more recently by Malherbe (Nantes) and Fossion; and admitted by J. Béclard ("Physiologie," 6th ed., 1870). Now, it appears incontestable that the contraction of the papillary muscles transforms the auriculo-ventricular cone, that is, the infundibulum left between the opposite sides of the valves, into a veritable tendinous cord, more or less hollow, between the interstices of which the blood is unable to make a passage by which it may flow back into the auricle.[1]

What becomes of the blood thus pressed between the sides of the ventricle and the hollow piston which penetrates its cavity? Under the influence of the contraction of the ventricle and of the working of the auriculo-ventricular system, which acts as an *expulsive apparatus*, the cavity of the ventricle has a tendency to completely disappear, even to its base, by means of the fleshy columns (columnæ carniæ) whose contractions bring the edges of this base in contact with that of the auricular *plunging cone.* The blood, being unable to return into the auricle, must escape by the arterial orifice of the ventricle (pulmonary artery or aorta). We must, however, observe that these arteries are already, by means of the foregoing contraction, filled with blood subjected to considerable pressure, which may be estimated at one-fourth of an atmosphere (see further on). We can easily conceive that, in order to overcome this pressure, great force is required on the part of the ventricle: it therefore contracts slowly and with much force. Contrary to what we have seen in the case of the auricle, *the ventricular systole occupies quite an appreciable space of time.* It is for this reason, also, that the walls of the ventricles are much thicker than those of the auricles, and in proportion to the resistance there is to be overcome, those of the left ventricle being thicker than those of the right.

Thus the pulmonary artery (or aorta, left ventricle) is forced to receive the blood which the ventricle pours into it. *The ventricle is completely emptied:* its contraction is no longer necessary, and it is relaxed; it is now that the heart is still. We represented the total duration of a cardiac revolution by *five:* the first fifth being occupied by the contrac-

[1] This theory has lately furnished a lively discussion in the Académie de Médecine (Gaz. Hebd., 10 Avril, 1874).

tion of the auricle (one-fifth); the three following fifths, by the contraction of the ventricle (three-fifths); in the last fifth, the heart being in entire repose (see the table, p. 141). We know that during these four latter fifths (three-fifths of ventricular systole and one-fifth of total repose) the auricle is quite still. Speaking generally, the revolution of the heart is divided into three periods: the first, of auricular systole; the second, of ventricular systole; the last, of entire repose. The typical length which we have assigned to these three periods may vary greatly, according to circumstances and individuals, and even in animals: the second period, that of repose, presents the greatest number of varieties: among the cold-blooded animals, the batrachians particularly, there is a long interval of repose after each contraction of the heart.

But why, when the heart is in repose, does not the blood which has been driven into the artery return to the ventricular cavity? Because the arterial orifice (pulmonary or aortic) is furnished with three semilunar or sigmoidal valves, which are thrown out by the retrograde pressure of the blood, and completely close the corresponding orifice. There is no need of a lengthened explanation of this mechanism, which is plain to any one who examines the organ. At the moment when the blood has a tendency to flow back again, the *gusset*-like form of these valves, the orifice of which is turned towards the arterial cavity, presents a sort of trap to the blood, by which the valves are forced out, and thus occlude the passage. The *nodule of Arentius*, which is placed in the middle of the free edge of each of these valves, has, no doubt, the effect of making the occlusion more complete.

To sum up:—

1. The auricle contracts instantaneously and without much force, that it may throw the blood into the ventricle, which is only too ready to receive it. At all other times the auricle is in a state of relaxation, of slow and progressive distention, which produces the effect of blood-letting at the terminal extremity of the venous system.

2. The ventricle contracts strongly and slowly, on account of the resistance which it has to overcome, and which is occasioned by the tension of the blood by previous contractions accumulated in the arteries.

The auriculo-ventricular valves are not valves, but an entirely distinct apparatus.

The semilunar valves are true valves.

Sounds and Impulse of the Heart. — Hitherto we have

made use indifferently of the words "right" or "left heart," "aorta" or "pulmonary artery," because all that is said of the right heart applies equally to the left, and there are no more valves in the pulmonary veins than in the vena cava.

The phenomena which we have examined in the two hearts are manifested outwardly by *particular sounds* (*first and second sound of the heart*) and by the *impulse or shock of the heart;* there are *one impulse* and two sounds to every cardiac revolution.

The impulse of the heart (or shock) consists in a tremor which we feel against the walls of the thorax: by placing the hand upon the sixth rib, to the right of the nipple, we feel that the heart seems, as it were, thrown at each contraction against the side, like a hammer upon an anvil. But there is really no blow, in the proper sense of the word, because the point of the heart always touches the wall of the thorax, and there is never any separation between them. Indeed, such a separation is inconceivable, there being nothing to fill the void which it would occasion, nothing to interpose between the heart and the thorax, not even the lung, for there are, in general, four pulsations of the heart to one expansion of the lung. There is thus, at each apparent shock, only a more decided contact between the heart and the corresponding part of the chest wall. Many theories have been adduced to explain this phenomenon, the most generally received of which is that of Hiffelsheim, *theory of recoil* (*du choc en retour*). The shock, received by the heart at the instant that the contents of the ventricle are expelled, is compared to the recoil of a gun when it is fired. But this shock is felt on whatever side the heart is touched, even at its lowest part through the diaphragm; this simple experiment refutes the theory of recoil, as not being always applicable; and also overthrows that which is founded on the straightening of the arch of the aorta, under the influence of the flow of blood, the more so because this shock to the heart takes place even in animals which have no arch to the aorta.

The *movement of the heart* may be best described by remembering the changes in form and consistency which the ventricle undergoes at the moment when the systole takes place: it passes from a state of relaxation into one of contraction, and presses strongly upon its contents in such a manner as to force them into the arterial tree, which already contains blood under tolerably strong tension. Even if the

thorax of an animal be opened, and the heart taken out with the hand, this change of consistency, coinciding with the ventricular systole, may be felt over the whole surface: the *pulsation of the heart* is then felt, as when the hand, placed over the cardiac region, feels it through the wall of the chest. The *displacement*, the *recoil*, and even the *torsion* of the heart thus have little to do with producing the shock felt; it is principally owing to the change in the condition of the ventricle, which, at first flabby and soft, stiffens throughout in order to expel its contents.

In the auscultation of the heart we hear, during one of its contractions, two sounds succeeding each other at short intervals. It has been demonstrated by a long series of vivisections that the *first sound* is produced during the systole of the ventricle, and the *second* immediately after the systole, when the heart enters a state of complete repose. We are agreed as to the explanation of the *second sound:* as it is produced during the repose of the heart, it is evidently not caused by any movement in that organ. It is, therefore, in general, rightly attributed to the movements of the aortic and pulmonary (semilunar) valves, which stiffen suddenly in arresting the backward flow of the blood. This sound is short and sharp (theory of Rouanet).

It is more difficult to explain the *first sound.* It is generally supposed to be owing to the play of the auriculo-ventricular valves; but if these membranous folds really act as valves, they ought to stiffen suddenly; and as, moreover, the first sound lasts a certain time, nearly corresponding with that of the contraction of the ventricle, its intensity and its length can only be explained by supposing it to be caused by the muscular contraction of the walls of the ventricle. If, on the other hand, we call to mind the description given of the working of the auriculo-ventricular apparatus, and take into account the resemblance of this sound to that of a sail flapping in the wind, or of a towel suddenly tautened when stretched out by the four corners, its explanation becomes simple. It is a sonorous manifestation of the working of the membranous auriculo-ventricular sails, stretched out by the papillary muscles and their tendons, as long as the ventricular systole lasts. These long, jerky, and energetic tensions are exactly what would produce the sound which we have described.

In order to sum up the relative length of the auricular and ventricular systoles and diastoles, we will, with a line divided

into five parts representing the length of a cardiac revolution, register, as follows, the time of each of these movements and of the corresponding sounds:—

	1	2	3	4	5
Auricle.	Systole.	Diastole or repose.			
Ventricle.	Repose.	Systole.			Repose.
Sounds.	Silence.	1st Sound.			2d Sound.
Shock.		Impulse.			

II. Peripheric Organs of the Circulation.

A. Mechanical arrangement of these organs.

We have seen that there is an artery which begins in the ventricle, and becomes, as it continues, more and more ramified (A). In a mechanical or hydrostatic point of view we may leave out of consideration the ramified form of the arterial tree (Fig. 40); that is, in placing all the arterial trunks (B) in juxtaposition, we need not take into account all the partitions which result from placing the vessels side by side (C). Now, as it is proved that when a vascular trunk is divided, the sum of the containing space in the two branches is always greater than that of the primitive trunk; so that the capacity of the system increases the farther it is removed from the aortic trunk, we obtain, in the diagram made as above described, a *conic figure of the arterial system* (Fig. 40 C). This cone will spread out like a tent, and the widening will be considerable at the arterial extremities (base of the cone), because the bed in which the blood circulates is greatly enlarged as it approaches the capillaries (Fig. 41). The same principles being applied to the venous system, *the latter may be theoretically represented by a cone placed with its base in opposition to the cone of the aorta*, the common base representing the capillary system, and thus forming a short cylinder placed between two cones

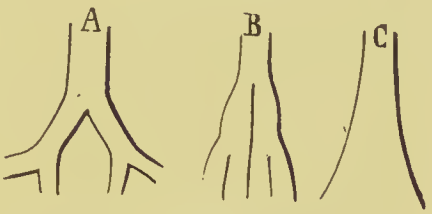


Fig. 40.
Diagram of a vascular cone.*

* Construction of a vascular cone, an arterial cone, for instance. A, Artery, bifurcated repeatedly. In B the bifurcated branches are supposed to be brought close together, giving rise to a partitioned cavity. In C, by removing these partitions, we find that the whole of the primitive trunk and its divided branches form a cone.

(Fig. 41). As regards their relation to the heart, we have seen already that at the summit of the arterial cone is found a muscular reservoir, the left ventricle; and at the summit of the venous cone a similar reservoir, the right auricle. This constitutes the system of general circulation, *the greater circulation*. In addition to this double cone, as representing the general circulation, a similar one may be placed representing the pulmonary circulation: as in the case of the first-mentioned system, the two extremities of this double cone will each communicate with a muscular reservoir; the right ventricle on the one hand, and the left auricle on the other. By giving these two systems of cones a curved form, so as to bring their different summits to the same central point, as is the case with the heart in the living body, a graphic description of the whole circulatory system may be given, under the figure of two incomplete circles joined at their free extremities, thus forming a sort of figure of 8 (Fig. 42).

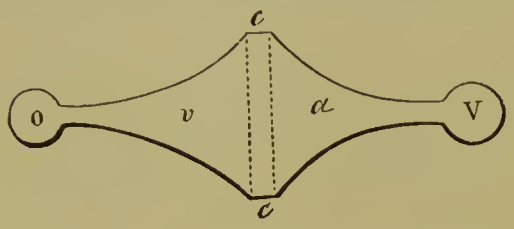


Fig. 41.—Diagram of the whole extent of the arterial and venous cone, with the interposition of the capillaries.*

This figure shows plainly that the four muscular reservoirs which form the heart are so arranged that the pulmonary double cone is in communication with the double cone of the general circulation. For this purpose the left auricle, communicating with the system of the pulmonary veins, opens into the left ventricle at the beginning of the system of the general circulation; this is the left heart. On the other hand, the right auricle, communicating with the general venous system, opens into the right ventricle at the point of departure of the pulmonary arterial cone; this is the right heart.

Knowing the mechanism of the heart, we can, by means of this simple sketch or diagram of the peripheral organs, account for the *circulation*, and determine the two essential conditions of the blood when in motion; these are its *pressure* and its *velocity* in the different parts of the circulatory apparatus.

Pressure.—At each contraction the ventricle pours from

* V, Ventricle. O, Auricle. *a*, Arterial cone. *v*, Venous cone. *c*, *c*, Capillaries.

180 to 200 grammes of blood into the system of the arterial cone, the effect of which is to maintain in it a pressure equal to one-fourth or one-fifth of the weight of the atmosphere. The auricle, on the contrary, being placed at the summit of the venous cone, has the effect, by its relaxation, of diminishing the pressure and nullifying it at the extremity of the cone; we have, indeed, already compared its effect to that produced by blood-letting. There results a gradual lessening of the pressure in the interior of the hydrostatic apparatus formed by the two cones; this diminution of pressure causes the blood to circulate from the left ventricle to the right auricle: in other words, the want of equilibrium gives rise to a constant current towards the point where the pressure is feeblest.

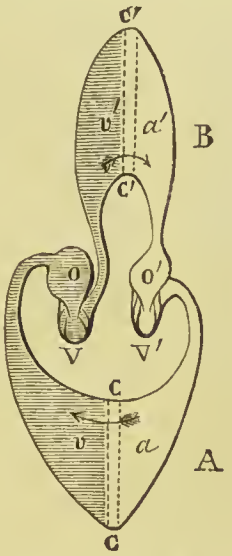


Fig. 42. — Diagram of the greater and lesser circulation.*

The pressure of the blood, at any point of the circulatory apparatus, corresponds to the distance at which this point is placed from the ventricular and the auricular summit of the double circulatory cone: the pressure is greatest ($\frac{1}{4}$ or $\frac{25}{100}$ of the atmosphere) at the level of the ventricular summit, that is, in the aorta; in the auricular summit, that is, in the vena cava, it may be said to be 0 (or $\frac{1}{100}$) of the atmosphere. It will thus be $\frac{12}{100}$ in the capillaries, which are placed half-way between these two extremities. At any other point in the arteries it may be represented by any number between $\frac{25}{100}$ and $\frac{12}{100}$, according to the position of the point under consideration, and the case is the same with regard to the venous cone. Thus, when an artery is opened, especially near its beginning, a jet of blood is seen which rises to a great height (as much as two meters); while from an opening made in the veins the blood only drops, unless artificial pressure is applied, as, for instance, by placing a ligature on the veins (as is done before bleeding the arm).

* A, *Greater circulation.* V′, Left ventricle. *a*, Aorta and its arterial cone. *c*, *c*, Capillaries of the body in general. *v*, Veins which go to form the vena cava (venous cone). O, Right auricle.

B, *Lesser circulation.* V, Right ventricle. *v′*, Pulmonary artery, with its divisions (*arterial cone of the lesser circulation*). *c′*, *c′*, Pulmonary capillaries. *a′*, Pulmonary veins (*venous cone of the lesser circulation*). O′, Left auricle. (The shaded part of the figure represents that part of the vascular system which is filled with blood from the veins.)

These differences in the lateral pressure effected by the blood upon the walls of the vessels through which it passes may be more correctly ascertained by placing different parts of the circulatory system in communication with a manometric apparatus, called, when applied to this special use, a *hemodynamometer*. The first hemodynamometer, employed by Hales, consisted of a long tube, which this physiologist introduced into a vessel, and in which the blood rose to a height proportioned to the pressure. This instrument has been greatly improved, and a mercurial manometer is now employed, in which, in order to avoid the coagulation of the blood, the column of blood is separated from the mercury by a column of some alkaline solution (solution of carbonate of soda), which prevents the too speedy consolidation of the fibrine (Fig. 43).

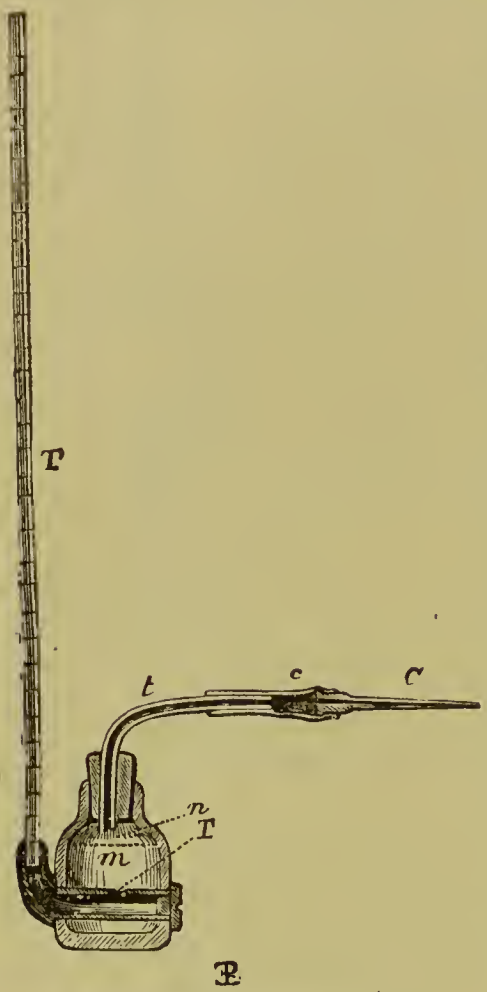


Fig. 43. — Hemodynamometer (or cardiometer).*

The pressure of the atmosphere for the larger arteries has thus been found to be about one-fourth; for those which are farther from the heart, as the humeral artery, one-sixth, and so on. In the

* This instrument consists of a thick, heavy glass bottle. At T is a tube, open at one end: the other extremity of the tube leaves the bottle, and is bent upwards, receiving at *n* a graduated glass tube (T). The lower part of the bottle and the beginning of the graduated tube are filled with mercury.

The upper part of the bottle is closed by a stopper containing a tube (*t*), which is joined to a metal tube *c*. The latter passes into the vessel in which the pressure is to be measured.

When the instrument is in action the whole upper part of the apparatus C, *c*, *t*, is filled with a solution of bicarbonate of soda, in order to prevent the coagulation of the blood. The pressure effected by the blood upon the surface of the mercury is communicated through the opening T to the mercury in the graduated tube, and by this means the tension of the blood is measured.

This instrument (Magendie's cardiometer) has, over the manometers usually

veins, on the contrary, the pressure is found to be extremely feeble, as an examination of the above diagrams has shown. The pressure in the capillaries cannot be measured exactly: it is, probably, as we have said, $\frac{12}{100}$ of the atmosphere. In hemorrhage from the capillaries, however, the blood does not come out in jets: its flow is here greatly retarded by the friction which it undergoes against the walls of these small tubes. If we examine the circulation of the capillaries with a microscope, we shall see that all the external portions of the blood current as it flows adhere to the walls of the vessels, almost without motion (passive layer); the central column alone moves, drawing with it the globular elements of the blood, especially the red globules; for the white globules, which are extremely viscous, are easily caught, and arrested in the passive layer (Fig. 44).

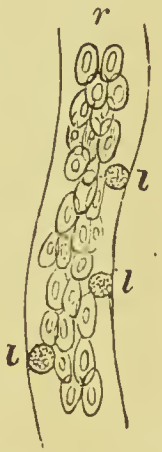


Fig. 44.—Capillary vessel of the interdigital membrane of a frog.*

These ideas as to the distribution of pressure in the circulatory system, though so simple, were not easily acquired. Poiseuille at first maintained that the pressure was the same at all points of the circulatory system, at whatever distance from the ventricle. This view, which reason alone might have shown to be an error, was experimentally overthrown by Marey; who has demonstrated that in the vascular system, from the heart to the capillaries, the pressure is distributed as in a liquid placed in a tube with one end open, and the other communicating with the bottom of a vase filled with liquid at a certain pressure. Poiseuille had also imagined that the general pressure varied in animals of different bulk, and always in proportion to their size. But Claude Bernard has demonstrated that this is not at all the case since the same apparatus with which we measure the mean or minimum pressure in a rabbit is quite sufficient to measure the same pressure in a horse. But, by means of the cardiometer, he has also shown that two things must be distinguished in the

employed (Poiseuille and Ludwig's instruments), this advantage, that it records exactly the cardiac pulsations; because the mercury, in this case, fills a comparatively large bottle, and not simply a tube in the shape of a U; and the whole mass of the mercury is not displaced at every change of pressure; neither does that friction take place which is produced by the loss of a large part of the force to be measured.

* *r*, Central current of the red globules. *l*, *l*, *l*, Peripheral layer of the blood current, in which the white globules move more slowly. (280 diam.)

pressure of the arterial system: 1, What we have called general pressure, minimum pressure; 2, The oscillations which this pressure undergoes at every fresh projection of blood from the ventricle. By the appreciation of this new element, these rhythmic *maxima*, Poiseuille's idea is justified up to a certain point: — the pressure varies in different animals owing to a variety of causes, among which size holds no unimportant place (Cl. Bernard).

Velocity. — The velocity and the pressure of the blood at any given point do not always exactly correspond: we have seen that by stopping the flow of blood in a vein we increase the pressure. The pressure at any given point depends on the distance of this point from the extremities of the double circulatory cone; while the velocity, on the contrary, depends on the form and width of that part of the circulatory cones in which the point is situated. In other words, and this is easily understood, the rapidity of the movement of the blood is in proportion to the space contained in that part of the tube under consideration. It must be remembered that we always speak of the united tubes under the appellation of the double cone. Thus, where the circulatory system is very large, as at the base of the cones (the region of the capillaries), the blood circulates slowly; exactly as the current of a river slackens greatly as the river widens, — into a lake, for instance: thus *the capillaries form the lake of the blood-torrent.* The maximum of the velocity is, however, attained in the narrow orifices through which the blood flows, that is, towards the summit of the cones in the aorta and in the vena cava.

These conclusions have been verified by direct experiment. The speed in the capillaries has been measured by microscopic examination of the small vessels of the frog, for instance; or by examining with the ophthalmoscope the capillaries in the retina of man; wherein the blood globules can be distinctly traced, and the time necessary for them to traverse a given distance calculated; it has thus been decided that the speed in the capillaries is only from one-half to one millimetre a second. This is trifling, compared with what we shall find in the larger vessels, but we must bear in mind, not only that the capillary system, taken altogether, forms *the lake of the blood-torrent*, but also that this lake is subdivided into a mass of fine net-work, friction against which deprives the liquid of much of its impulsive force. The influence of this friction, of this adherence to the walls of the capillaries, is fully shown by the researches of Poiseuille on the flow of the

liquids through tubes having a small diameter. They may be summed up in the two following laws: *the quantities flowing are to each other as the fourth power of the diameters of the tubes; they are in inverse ratio to the length of the tubes.* Now the capillary vessels, in addition to their net-like arrangement, form very long tubes, and thus unite all the conditions necessary to slacken the flow of the blood and prolong its contact with the tissues.

In order to estimate the velocity of the blood in the large vessels, special instruments are employed; or else a glass tube filled with an alkaline liquid is substituted, and placed at a certain point in an artery of large diameter, the time being then determined necessary for the blood to drive the liquid in question from the tube and afterwards traverse the known length of this artificial channel. This apparatus is the *hemodromometer* (of Volkmann) (Fig. 45), and is composed of a glass tube (A), bent like a horse-shoe, furnished at each end with a metal spout having a cock, and communicating with a straight metallic tube inserted in the two ends of the artery (a, a'). The tube being filled with the alkaline solution, and all communication with the artery (Fig. 45, No. 1) is shut off by means of the cocks (having three outlets); this causes the blood to follow the metallic tube; the two cocks are suddenly turned, and the blood is thereby forced to deviate from its course and enters the glass tube (Fig. 45, No. 2), which it traverses to gain the other end of the artery, driving before it the column of colorless liquid. An apparatus which is quite as ingenious, called the *hemotachometer* (of Vierordt), consists of a small transparent box (Fig. 46), placed in a portion of the artery. In this box swings a pendulum, which the current of blood causes to swerve to one side; this deviation increases with the rapidity of the current, and by its degree we can calculate the velocity of the blood. These experiments show that the velocity of the blood is 0m. 33 (thirty-three centimetres)

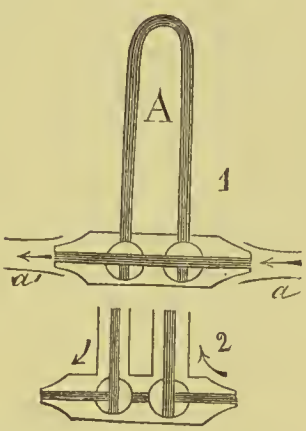


Fig. 45. — Volkmann's Hemodromometer.

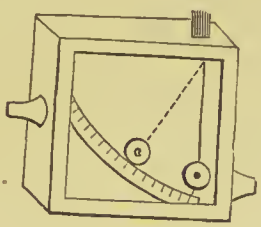


Fig. 46. — Vierordt's Hemotachometer.

a second in the carotid artery, and 0m. 44 in the aorta: it is also four hundred times greater in the latter vessel than in the capillaries. Similar results have been obtained with the *hemodromometer* of Chauveau, and the *hemodromographer* of Lortet (Fig. 47), which are constructed on the same principle as Vierordt's instrument.

By means of the above data on the velocity of the blood we can calculate the dimensions of the arterial cone. Indeed, the velocity at the different points of the cone are in inverse ratio to the surface of the section of the cone at this point: the total containing space of the capillary system is thus to that of the aorta as 400 to 1. We may therefore conclude that the containing space of the aorta having a diameter of 3 centimetres, the diameter of the base of the arterial cone must be about 0m. 66. If the exact capacity of this cone were known, it would be easy to calculate its height. These calculations, however, yield only approximative results, for the slackening of the current of the blood at the level of the capillaries is also an important feature, which is not here taken into account: it is caused by the net-like arrangement of long and narrow tubes (see the two laws of Poiseuille, p. 147, above).

It may still be asked, after determining the velocity of the blood in certain points, what is the general speed, considering the circulation as a whole? In one word, how much time is necessary for a blood globule to pass from the left ventricle to the right auricle? The average quantity of blood thrown into the aorta at each contraction of the heart is 180 grammes. As the total mass of the blood is only 5 kilogrammes, 25 or 30 cardiac pulsations are necessary to enable all the blood to pass through the central organ, and rather more than 30 seconds for the return of a globule which has left the heart. The result of this calculation can only be general and approximative; for the blood which goes to the lower limbs has a much longer passage than that which passes into the arteries and cardiac veins: the time of the complete journey (going and returning) of a blood globule must therefore vary, according to the part to which it is sent. Still, the circulation must always be extremely rapid, as is proved by experiment in cases of poisoning; for we know that a drop of prussic acid upon the conjunctiva will kill an animal in eight or ten seconds, and that the poison is found to be diffused through the whole system. If the poison is placed further from the heart, upon a wound in the foot, for instance, death

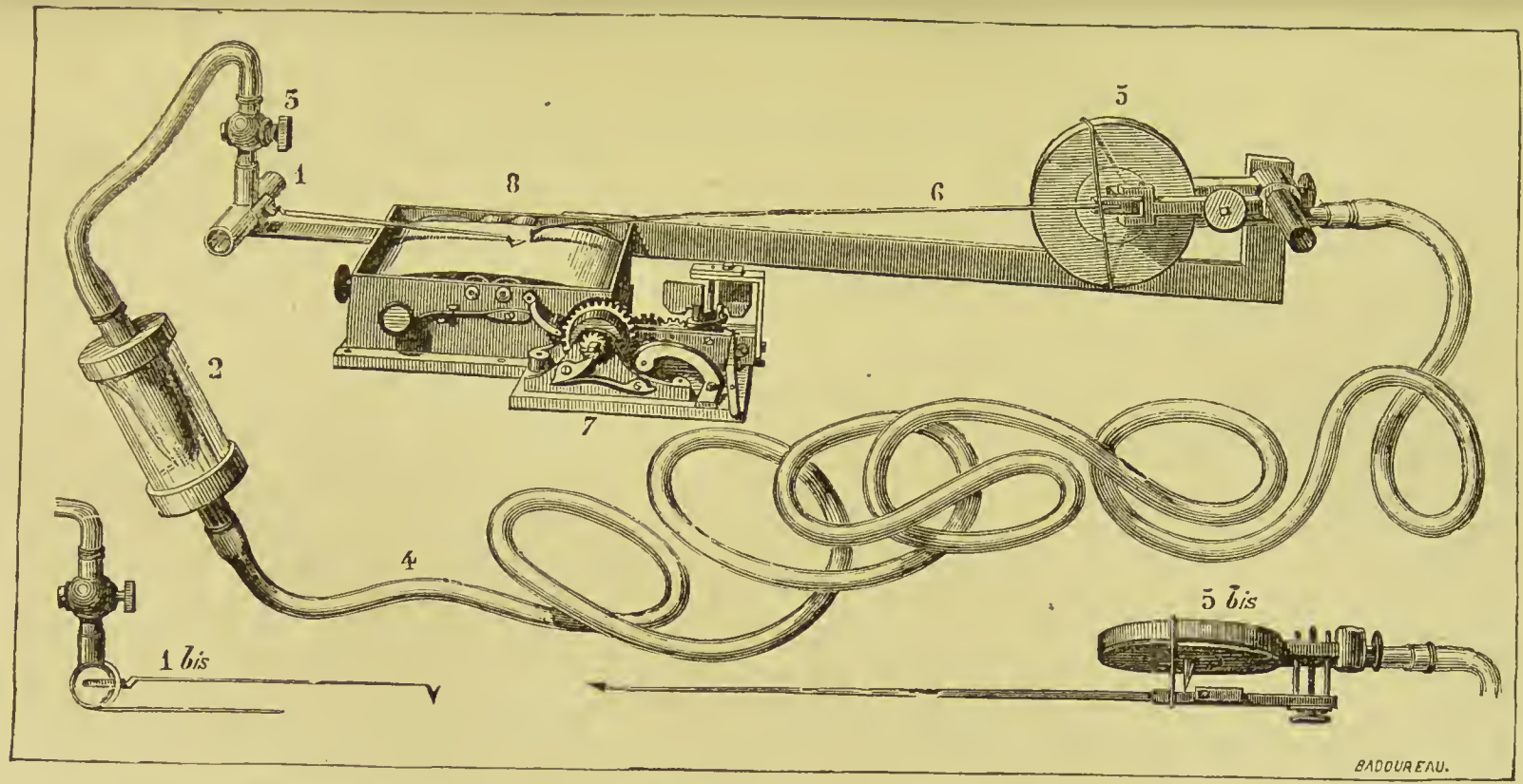


Fig. 47. — Chauveau's Hemodromographer. — 1, Metal tube, through which the arterial current passes. 1 *bis*, The hemodromographic apparatus in detail. 2, Marey's sphygmoscope, by which the line of the pulsation is recorded simultaneously with that of the velocity. 3, Cock by which the blood is allowed to flow, or prevented from flowing, into the sphygmoscope. 4, India-rubber tubing, through which the pulsation is transmitted to the registering apparatus. 5, Small drum, upon which rests the lever 6, that amplifies and marks the pulsations. 5 *bis*, The drum and lever in detail. 7, Registering apparatus, consisting of clockwork and a strip of paper, 8, which unrols below the two levers of velocity and pulsation, and on which the two lines are drawn simultaneously. One-third the natural size. (Lortet, "Annales des Sciences Naturelles.")

does not ensue quite so soon, because the blood takes more time to return by the saphenous than by the jugular veins. The standard experiment consists in injecting yellow cyanide into the central end of the jugular vein, and collecting the blood which flows out at the peripheral end. We find that, after the lapse of from eight to fifteen seconds, the poison appears at this end, the blood beginning to show the characteristic reaction of prussian blue (with salts of iron).

Special Arrangement of the Circulatory System in some Organs. — Such are the general conditions of the circulation, of its pressure and its velocity at different points. But the system of cones which we have been considering is not always everywhere so simple, and we find, in different parts of the circulatory apparatus, arrangements and conditions which are purely physical and mechanical, and which modify the rapidity of the course of the blood. Such are the great number of tubes, the clusters of capillaries, called the *retia mirabilia*, the type of which is an artery suddenly divided without altering its normal or regular dichotomic disposition. The result of this increase at any one point of the capacity of the vessels is a widened cone and a sudden diminution in the rapidity of the circulation of the blood. This is what takes place in the kidney, as we shall see later, at the level of the vascular pouches, called *the glomerules of Malpighi:* the effect of this disposition, in slackening the flow of the blood, is to increase the surface of transudation; this transudation takes place under special conditions of pressure (Fig. 48). We find something similar in the system of the vena porta: the blood furnished by the cœliac axis and the mesenteries to the organs of digestion is brought back by a number of veins into a common trunk, called the portal vein, which, instead of emptying immediately into the vena cava, is first distributed in the liver in the same manner as an artery, and forms the afferent vessels of the liver, the capillaries, and, finally, the efferent vessels, or hepatic veins, which flow into the vena cava. This whole system may be theoretically represented by a cone (Fig. 48) beginning at the trunk of the aorta, and representing the arteries of the intestines, with their capillaries. This arterial trunk is succeeded by a venous trunk, showing the origin and the trunk of the portal vein; this second cone is followed by a third, arranged in the same manner as an arterial cone (the circulation in which is from the top to the bottom), and representing the ramifications of the portal vein in the liver; at its

base (hepatic capillaries) this cone forms a fourth, representing the hepatic veins. In making this passage the blood, therefore, must traverse a system containing twice as many cones as the general system, and is subject at each double base (each network of the capillaries) to the slackening which we have mentioned.

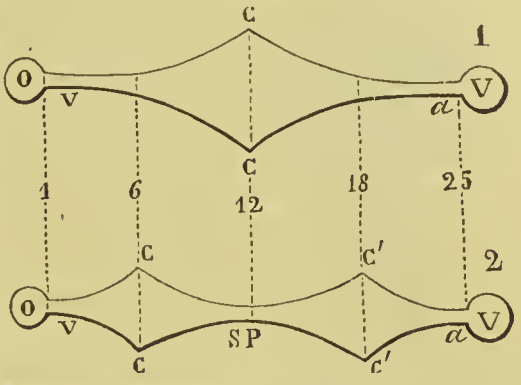


Fig. 48. — Diagram of the double cones of the portal system.*

The capillary vessels which are placed in the series of cones of the portal vein, moreover, have not the same pressure as the ordinary capillaries. As these systems are not placed at an equal distance from the left ventricle and the right auricle, neither can have a pressure half-way between $\frac{1}{100}$ and $\frac{25}{100}$ of an atmosphere. The pressure will be less in the hepatic capillaries, because they are nearer the auricle; and greater in the intestinal capillaries, because they are nearer the left ventricle. The latter condition, as we shall see, is not favorable to the theory of intestinal absorption by simple osmosis. We shall see also that the same theory may be asserted with regard to the capillary system of the kidneys.

B. Properties and Functions of the Vessels.

The general conditions of the circulation of the blood, of its pressure and its velocity, which conditions are simply the result of the mechanical arrangement of the blood tubes, may be affected and complicated by the *physiological properties of the coats of the vessels, the arteries, capillaries, and veins.*

Arteries. — Anatomy teaches us that the arteries are composed of three coats or tunics (Fig. 49). Of these three the most interesting to the physiologist is the middle tunic: it contains two essential elements, *elastic tissue* and *muscle*

* The superposition of the two diagrams shows that the pressure is not the same in the capillaries of a portal system and in those of the circulation in general.

1, *General circulation.* V, Ventricle. O, Auricle. *a*, Arteries. *v*, Veins. C, Capillaries (pressure 12).

2, Portal system. V, Ventricle. O, Auricle. *a*, Arteries. *c' c'*, First system of capillaries (pressure = 18). S P, Portal trunk. *c c*, Second system of capillaries (pressure = 6). *v*, Vein.

(smooth muscle, contractile cells). The first of these elements, elastic tissue, is found, with slight exceptions only, at the summit of the arterial cone, the aorta being formed almost entirely of yellow elastic tissue. On the other hand, the muscular element predominates largely at the base of the cone; that is, in the coats of the small arteries which precede the capillaries. In the intermediate parts the elastic and muscular tissues both share in the composition of the middle tunic, in proportion to the distance at which the point under consideration lies between the base and summit of the cone; so that a diagonal line, dividing obliquely the thickness of the walls of the arterial cone, represents exactly the comparative richness in elastic and muscular tissue of the different parts of the arterial walls (Fig. 50).

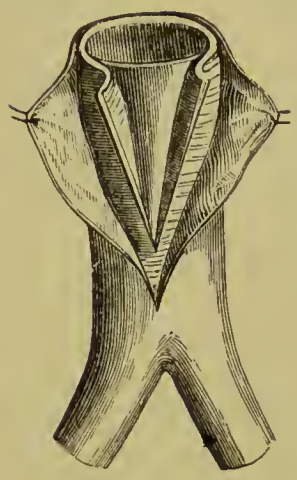


Fig. 49. — Artery in which the three coats are dissected.

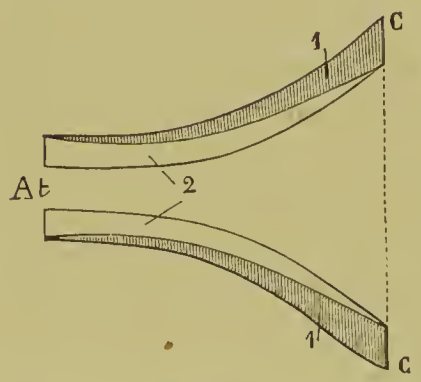


Fig 50. — Arterial cone; composition of the arterial coats.*

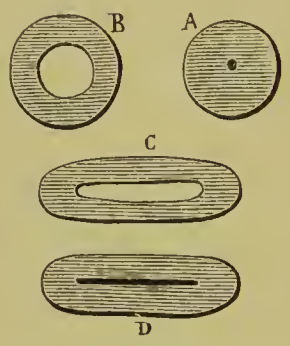


Fig. 51. — Natural form of the arteries.†

The arteries are, owing to the presence of the muscular and yellow tissue, extremely elastic tubes. This fact alone

* Proportion of the elastic and the muscular element in the composition of the coat of the cone from summit (At) to base (*c*, *c*). 1, Muscular element. 2, Elastic element.

† Element by which the natural form of the arteries is determined. A, Appearance of the section of an artery, supposing it to be formed of muscular tissue only. B, Section of an artery supposed to be of elastic tissue only. C, D, Section of an artery, showing its actual ribbon-like form, which is the physiological result of the struggle between these two elements, the elastic and the muscular.

indicates that they have a natural form, to which they are constantly tending to return, and which is antagonized by the force of the circulation. Moreover, they are not, as we should be likely to suppose, hollow cylinders, but rather hollow ribbons, with flattened sides. An artery of middle size contains muscular and elastic tissue in about equal parts. If there were only muscular tissue in the arteries, as this is arranged in circular layers like a sphincter, the whole central opening in the artery, on assuming its natural form of repose, would be a point or axial line, serving only as an indication of the canal (Fig. 48, A). The elastic tissue has a tendency to keep the artery wide open, and, if this alone existed, it would have the appearance of a large cylindrical canal (B). By a sort of compromise this constant antagonism between the elasticity of the muscle and the elastic tissue produces an intermediate form between these two extremes, that of a cylindrical, flattened ribbon (C, or rather D) slit transversely.[1]

This natural form is constantly opposed by the mass of blood which the ventricle at each systole causes to gush into the arterial system; the arteries, when full of blood, have also the form of a cylindrical tube; but we know, too, that they change their form according to the greater or smaller quantity of blood which they receive. In cases of severe hemorrhage, they assume their natural *ribbon-like form;* they assume it also, after death, by ejecting their contents into the capillaries and the veins; thus the arteries of a dead body are empty and flat. We must, however, add, that they preserve this form in the dead body, only when the air has not entered their interior. Directly any opening is made in their coats, they begin to draw in the air, and to assume the appearance of hollow cylinders. This fact is easily explained: after the last pulsation of the heart, the arteries still endowed with their vital activity have, by ejecting their contents into the veins, taken the natural form of a hollow, flattened ribbon, which form is due to the antagonism between the muscular and elastic tissue; the muscular tissue, however, soon loses its properties, and from that moment, in a physiological point of view, the artery is composed only of elastic tissue, the natural form of the artery of a dead body being consequently

[1] See Louis Oger, "*Considérations Physiologiques sur la Forme Naturelle et la Forme Apparente de quelques Organes, et en particulier sur la Forme Naturelle et la Forme Apparente des Artères.*" Thèse de Strasbourg, 1870, No. 283.

that of a hollow cylinder; the pressure of the atmosphere, however, prevents it from dilating and assuming this form, and it can only completely assume it when the air is admitted into its cavity by an incision.

Thus, during life, the arteries are in a state of permanent tension: this constitutes their *tonicity*, and is similar to what we have already studied in the sphincters, and in the muscles in general.[1] The effect of this peculiar condition is that the arteries do not serve simply to conduct the blood; they transform the circulation, changing the intermittent stream of blood which gushes from the heart, into a continuous flow. In the large arteries near the heart, the flow of the blood is still intermittent, but as we proceed farther into the arterial system, we find that it becomes continuous. Indeed, by deducting from the flow of the carotid artery that of the origin of the aorta, it has been calculated that each blood wave contains about 180 grammes of blood. This enormous

[1] These considerations as to the natural and the apparent form of an organ, of a simple tissue, or one composed of several elements, are of the highest interest in general physiology, and throw sometimes unexpected light upon the explanation of certain phenomena. We have already studied the muscle under two physiological forms (form No. 1 and No. 2) which they scarcely ever perfectly attain. There are certain ligaments, as the yellow ligaments of the vertebral column, which, also, scarcely ever attain their natural form. If the series of spinal apophyses and laminæ be divided from the series of the articulating masses by two strokes of a saw behind and throughout the length of the vertebral laminæ, and after this separation the length of the two vertical halves of the column be compared, we shall find that the back part has shortened in a very remarkable manner, the shortening corresponding nearly with the height of three vertebræ of medium size. The yellow ligaments are evidently the cause of this shortening; they are restrained by the separation and the rigidity of the laminæ upon which they are stretched, which prevents their assuming their natural form, and they can return to it only on the withdrawal of this antagonistic force.

We shall see that the natural form of the lung in the living body differs from the natural form of the lung in the dead body, and that in the living and normal organism the first is never found perfectly developed. This study will help us to comprehend easily the mechanism of expiration.

By the *natural form*, *either of a tissue or an organ*, must be understood *the form peculiar to the tissue or organ*, *independent of all foreign influences*, *more or less constant*, *which have a tendency to antagonize or oppose its peculiar form.*

quantity of blood must produce great dilatation of the aorta, the coats of which, reacting in their turn on the blood, drive it into the arterial cone, where, by a series of dilatations and successive windings, becoming less and less sensible, the flow of the blood which, in the summit of the cone, was *jerky*, becomes nearly *regular* in the region of the capillaries (base of the cone).

There is, thus, at the summit of the arterial cone, at each systole of the ventricle, a very sensible *wave*, which is still felt in the lesser arteries, and disappears in the capillaries. This phenomenon constitutes the *pulse*. The *pulsative wave* is very sensible to the touch in the radial artery: the *pulse* is thus the impression made upon the finger (sense of touch) by the approach of a wave.[1] A physician often produces, in fluids, phenomena exactly similar to that of the pulse, such as the *fluctuation* observed as the result from a sudden blow upon a pouch or bag filled with liquid; the heart produces a real percussion on the mass of the blood, by the shock of its systolic expulsion; the pulse, therefore, coincides with the beating of the heart, but follows it at a short interval; which is, for the radial pulse, one-seventh of a second, the time necessary for the wave to flow from the heart to the radial artery at the level of the wrist.

Under certain circumstances the *pulsative wave* is transmitted more or less strongly and rapidly, according as the arterial coats are more or less stretched out. If the coat be soft, the pulsation is transmitted slowly; and rapidly, if the coat, on the contrary, be hard and resisting. Thus a stone falling into the water produces waves more slowly in proportion to the depth of the water; if the water be covered with a layer of ice, the propagation of the waves will be more rapid. As the phenomena of *fluctuation*, observed in surgery, are more or less distinct, according as the coats of the pouch containing the liquid are more or less stretched (in a bladder which is too much distended, the flow of the blood can hardly be detected), so the state of the physiological coat (of the arteries), and especially the state of the arterial muscle, influences the form of the pulse. We know that, owing to the elasticity of this element, the arteries are not rigid, and this circumstance, while allowing the presence of the wave to be felt, finally exhausts it. (See above, that

[1] *Unda non est materia progrediens, sed forma materiæ progrediens.*

the elasticity changes the jerky movement of the blood into a regular movement); but if the muscle is paralyzed, and thus has lost its perfect elasticity, the gradual transformation of the intermittent shock into a continuous movement ceases; and we find that jerks occur in the smallest arteries, and even in the capillaries, as has been observed in the mesentery of the frog; the same takes place in inflamed tissue, and there are few persons who have not experienced the arterial, or rather capillary pulsations of a *whitlow*.

In all this, the pulsation, the arrival of a wave, must not be confounded with the movement of the circulation of the blood itself; we cannot repeat too often, — *unda non est materia progrediens, sed forma materiæ progrediens:* Czermak has proved, by very close examination (*sphymographe à miroir*), that, while the rapidity of the movement of the blood diminishes as we approach the capillaries (see page 132, above), the speed with which the pulsative wave is propagated increases, on the contrary, from the centre to the periphery, and that it is greater in aged persons and in adults than in children, showing that we must not confound the pulse, its rapidity and form, with the rapidity of the blood and the activity of its circulation. Onimus, in his *Etudes sur les tracés obtenus par le sphygmographe* (Journal d'Anatomie, 1866), has dwelt especially on these features of the pulsative wave.

The waves of the blood column may be ascertained by placing a manometer in communication with the vessel: *alternate rising and falling* is then easily observed. Efforts have been made to count these undulations by means of Ludwig's *kymographion* (Fig. 52), which is only a modification of the *hemodynamometer* described above. On the surface of the mercurial column of the manometer (in *a*, Fig. 52) is placed a small float, having on its upper face a vertical stem (*b*), articulating with a second horizontal stem (*c*), furnished with a point, which touches a turning cylinder (D D′) blackened by smoke. If this cylinder were immovable, the style would trace vertical lines; but, as it turns regularly, the lines traced are undulating, and, according as their convexity is in an up-

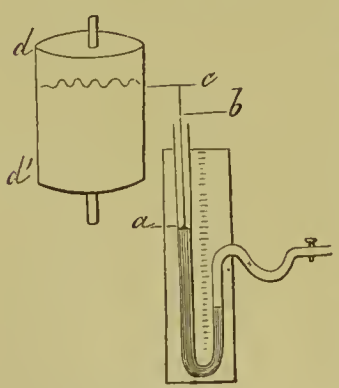


Fig. 52.
Ludwig's Kymographion.

ward or downward direction, they are called *positive* or *negative*, the former corresponding to the ventricular systoles, and the latter to the repose of the heart.

The sphygmograph of Marey, applied to the radial artery in man, gives similar results. This is a *registering apparatus*, noting down the impulsions of the artery imprinted upon it: this is done by means of a small lever, applied to the artery in the same manner as the finger of a physician when examining the pulse. The comparative duration of the systole and the diastole is decided by the length of one of these waves, as may also all the modifications of the circulation (Fig. 53). It has thus been shown that the *dicrotism* of the pulse, plainly sensible to the touch in some diseases, is only the exaggeration of a *dicrotism* constantly taking place in the normal condition of the blood wave. It consists in a slight elevation, seen in the line of descent in the diagram (Fig. 53, in *d*), and is a sort of second pulsation coming after the first. The investigations of Marey, Vivenot, and Duchek

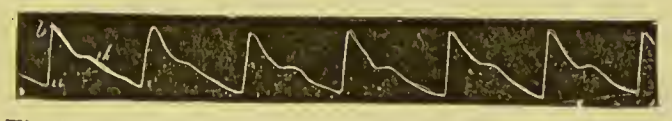


Fig. 53. — Sphygmographical tracing of the normal pulse.

have rendered the mechanism of this phenomenon plain. It was at first attributed to a *returning wave*, produced either by the closure of the sigmoid valves or by the reflux of a pulsation, which is reflected by the sharp division fold at the bifurcation of the aorta into the two iliacs. Every fact now seems to prove that the dicrotism is owing to the elasticity of the artery, which, having been distended by the ventricular systole, returns to its former size. The slight ascension, interrupting the line of descent (Fig. 53, *d*), marks the exact moment when, as we said before, the arterial elasticity restores to the blood wave the force which it had stored up, and which would be lost in a rigid tube, being expended in friction (see p. 155, above).[1] By means of the sphygmograph many other peculiarities of the circulation have been observed: for instance, in deep inspirations the negative waves increase in number, while they diminish when forcible expiration accompanies the strong pressure which takes place

[1] See Lorain, "Etudes de Médecine Clinique." Du Pouls, 1870, in 8vo.

in the thorax: the positive waves then increase (see Respiration). It has been thought that under certain circumstances the right pulse is more or less rapid than the left: this is what is called the *differing pulse*. This supposition arose from errors in observation. The difference is simply due to accidental rhythmical contractions of *satellite* muscles of the arteries, the coraco-brachial, for instance, in the case of the radial pulse.

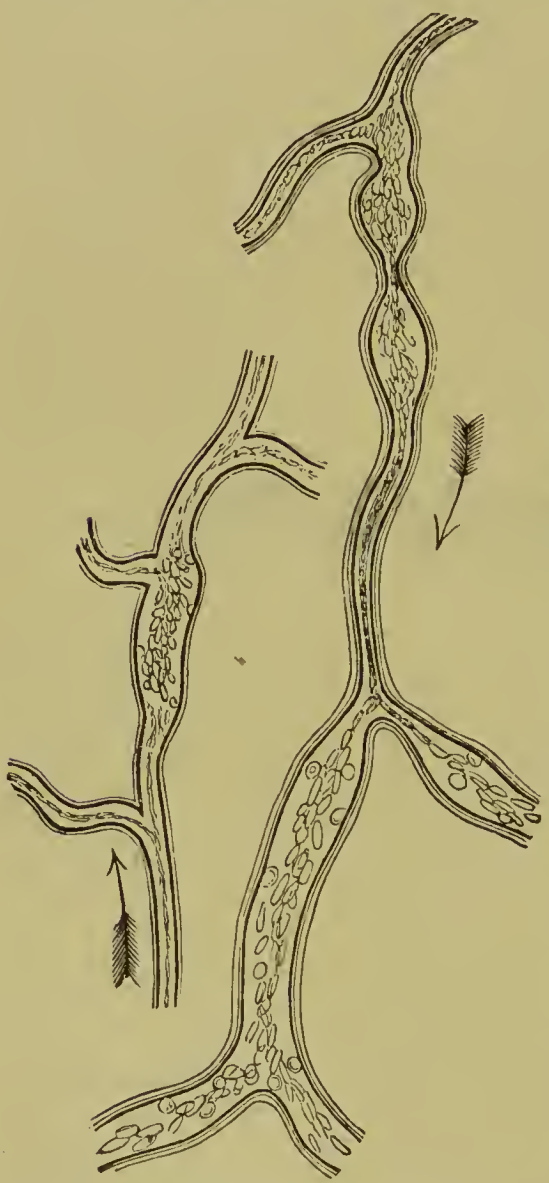


Fig. 54. — Contraction of the small arteries.*

Besides these elastic properties, belonging to the muscle and to the yellow tissue, by means of which the arteries regulate the general circulation, these vessels have also power, by the contraction of their smooth muscles, to change their size considerably, and in this way influence the circulation. As these muscles abound in the small vessels (see Fig. 50), it is principally the local circulations which are thus modified, these variations in diameter being scarcely observable in the large arteries. In general, the small arteries contract more or less, according as they may be more or less well nourished. These contractile properties are made use of in surgery, and the hemostatics employed are useful, not only because they coagulate the blood, but also because

* Irregular contractions of the small vessels of the interdigital membrane of a frog. The contraction is produced by irritation. (Wharton Jones.)

they excite the contraction of the small arteries, and thus diminish their size: cold, especially, serves to produce contraction, as may be verified in the mesentery of a frog (experiment by Schwann); in this case the small arteries diminish to one-seventh of their calibre (Fig. 54). In the normal state the arterial muscle is sometimes contracted, and sometimes relaxed; but, taking into account the variations in size, and the changes in the circulation resulting from them, we can in this only see rhythmical contractions calculated to assist those of the heart. The arterial muscle takes no part in the pulsation: in this phenomenon it is simply passive, as we have already shown.

Capillaries. — The diameter of these vessels is extremely small: in the smallest it is hardly sufficient to allow of the passage of a blood globule; the size, however, differs in different parts. The capillaries of the skin are large in comparison with those of the lungs or of the brain, and, on account of the size of the capillaries of the fingers, it is easy to inject through the arteries the commencement of the veins of the foot or of the hand.

The capillaries are generally formed of coats of very simple structure: their tissue is apparently amorphous, but traces of cellular structure are found in them, in the shape of laminated flattened plates, the remains of ancient cells, which have lost the principal physiological properties of the globular element when losing its form. The capillaries have not, however, perhaps, always distinct walls: this is probably the case with the capillaries of the liver, which are, apparently, only lacunæ hollowed out in the substance of this organ (interstices between groups of hepatic cells).

What we have already seen shows that, in general, the circulation is continued in the capillaries, and that the cardiac wave is felt in them only under exceptional circumstances. We have also studied and explained the presence of what is called the *inert layer* (see Fig. 43, above).

The capillaries are not contractile: their structure forbids our attributing this property to them, and all the phenomena of dilatation or contraction which we observe in them are entirely passive, owing to similar phenomena taking place in the small arteries and veins. The ancient physiologists believed with Bichat that the function of the capillaries was active, and that they are very contractile; they considered them as forming a *peripheral heart.* Glisson's capsule, a fibrous tissue surrounding the vascular network of the liver,

was, according to them, one of these organs of peripheral impulse, intended to aid the action of the heart. We can easily see, by our study of the circulation, that the contraction of the capillaries, the *so-called accessory hearts*, would be rather an obstacle than an assistance to the flow of the blood. The pulsations felt in an inflamed tissue (in a whitlow, for instance) were adduced as a proof of the rhythmical contraction of the capillaries, but we have already explained this sensation as being caused by a paralytic dilatation of the smaller arteries. We have also seen that the effect of hemostatic agents is to produce the contraction, not of the capillaries, but of the small arterial vessels. The so-called contractility of the capillaries thus belongs entirely to the region of theory, and rests on no positive fact; and the experiments made on the mesentery of a frog have reference to contraction of the small arteries, and not of the capillaries.

The capillaries, as we have considered them, form a perfectly well-defined part of the circulating system, and their physiological properties are quite distinct from those of the arteries and the veins: we consider as *capillaries*, with Köl-liker and C. Morel, only those small vessels, which, without undergoing any previous preparation, appear as tubes of an amorphous substance in which oval nuclei are inserted. Some histologists, however, Henle and Charles Robin in particular, class under this denomination both the capillaries properly so called, and the finest ramifications of the small arteries and veins. Thus Ch. Robin divides the capillaries into three kinds: 1, *capillaries properly so called*, distinguished by having a single homogeneous tunic with a nucleus, their diameter being from $\frac{7}{1000}$ of a millimetre (the diameter of a blood globule) to $\frac{30}{1000}$ of a millimetre; 2, *cœpillaries of the second kind*, having a diameter of from $\frac{30}{1000}$ to $\frac{70}{1000}$ of a millimetre, and provided with a double coat, the inner one being a continuation of the outer, which is formed of contractile cellular fibres arranged in circles; 3, *capillaries of the third kind*, their diameter being from $\frac{60}{100}$ to $\frac{140}{1000}$, and having, beside those already mentioned, a third external tunic formed of connective tissue. For the physiologist, these two latter kinds of vessels are evidently small arteries and veins, likewise possessing great contractility; they represent, exactly, the base of the arterial and venous cone, which abounds in smooth muscular elements, to the exclusion of the elastic element.

The structure of *the capillaries, properly so called*, is not,

however, so simple as an examination of them, without the use of reagents, would lead us to suppose: the researches of Auerbach, Eberth, and Aeby, and the method of impregnation by nitrate of silver, employed by Chrzonsczewsky, have proved that the capillaries are lined with a pavement epithelium (endothelium) exactly similar to that which forms the inner layer of the arteries and the veins: outside this endothelium the capillary coat is formed by a layer of cells, placed close together; so that we can no longer consider the capillaries as produced by the end to end fusion of cells, whose cavity would thus become the lumen (or interior space), and the membranes the coat of the capillary. This way of regarding the development of the capillaries was first suggested by Schwann and Kölliker, as the result of their experiments on the tail of young toads, and appeared to confirm the experiments of Balbiani on the cicatrization of wounds in the same animals; this theory, however, could not stand before the discovery of an *endothelium* in the cavity of the capillary; from that time, this cavity has no longer been looked upon as an *intracellular*, but as an *intercellular*, space. The study of its development (His, Afanasieff, Rouget) proves that the capillaries not only possess this endothelium, but that it is enclosed in another layer of cells: the coat of the capillaries, when in course of development, is composed on either side of two layers of cells placed end to end, in such a manner that the vascular cavity is a canal hollowed out between these double layers of cells.[1]

[1] The structure of the capillaries and the small vessels (small arteries and veins) does not as yet enable us to explain the phenomenon of *diapedesis*, or protrusion of the globules, which some observers have witnessed, and which many pathologists look upon as one of the sources of suppuration. We have seen that the white globules of the blood and the globules of the pus are exactly similar, as also the globules of the lymph, whence the theory arose that the pus globules were only white globules of the blood which had left the vessels. Cohnheim (1869) asserts that, in his investigations on inflammation of the cornea and the mesentery of the frog, this hypothesis was verified by experiment, and that he saw the *diapedesis* of the white globules. Hayem has made the same observations, and states, moreover, that diapedesis of the red globules also takes place, especially under the influence of an excess of pressure produced by ligature of the veins. This question of pathological physiology is too important to be passed over here, but it is at the same time one on which there is so much difference of opinion that we can only mention it. The theory of diapedesis has many partisans in the

These rapidly sketched histological details show that our present ideas might easily change on the subject of the properties of the globules, especially their contractility: their coats are composed of globules which have, no doubt, preserved the properties of the living globule: Stricker, indeed, has no hesitation in pronouncing these coats contractile; he asserts that he has demonstrated that the capillary coats of toads possess a contractility shown by alternate shrinking and enlargement, and thus believes himself authorized in attributing the same property to the capillaries of completely developed animals. If this view is confirmed, it will not be so necessary in future, in a physiological point of view, to distinguish the capillaries properly so called, from the small arteries and veins, and we may allow that there are several varieties of capillaries. (See p. 160.)

We will add, finally, that the investigations of Sucquet and Péan show that the communication between the arterial and the venous cone is sometimes made without the medium of the capillaries, by means of small intermediate vessels, visible to the naked eye, and abounding in muscular elements: it is asserted that these vessels sometimes contract, but under other circumstances dilate, leaving an easy passage to the arterial blood, which flows directly into the veins, the capillary circulation being reduced to its minimum, whence the name of *derivative circulation*. This disposition, which all anatomists have refused to admit until now (it is denied by Vulpian) is found, according to Sucquet, especially in the extremity of the fingers and toes, in the front of the knee and the back of the elbow, in the skin of the lips, the cheeks, the nose, the eyelids, the mucous membrane of the nasal chambers and of the tongue.

French schools: though rejected by Ch. Robin, it is held without any restriction by Vulpian and Charcot, who make it the basis of their teaching on the subject of inflammation. We must add that, in a course of experiments made personally, we have remarked the passage of the white globules only under exceptional circumstances, and when suppuration, which was already far advanced, had brought the vascular coats back into the embryo state. (See Duval and Strauss, "Archiv. de Physiol.," 1872.) Messrs. Feltz and Picot have also published observations opposed to the theory of diapedesis ("Journal de l'Anatomie" of Ch. Robin, 1871–1873).

See also a late monograph by Cohnheim, wherein he asserts the true nature of inflammation is not yet discovered, the passage of the globule being attributed to a secondary rather than a primary cause of the pain, heat, and redness.

Veins. — The structure of the veins closely resembles that of the arteries; they are, however, distinguished from them by containing much less elastic tissue, and thus have no tendency to remain open, even in the dead body, after the blood has run out.

These vessels are, nevertheless, very contractile, but the muscular element in them is unequally distributed. Their contractions may be easily observed; for instance, we see the veins of the hand contract and shrink when immersed in cold water; a sudden blow, or slight percussion of a subcutaneous vein, produces immediate contraction, followed shortly by paralysis which causes the vessel to dilate; and we sometimes see these two phenomena succeed each other irregularly. These contractions of the veins assist the circulation, but their rhythm is never regularly intermittent; there is really no systole or diastole, properly so called. The effect of the contraction is to diminish the size of the vessel, and to drive the blood always in the same direction, on account of the valves, of which we shall speak presently.

The veins are very dilatable, owing to the elasticity of the muscular elements which compose their coats, and we may say that one of their principal functions is to promote the easy flow of blood from the capillaries. Thus we see that the veins, beside taking the part of conduits, also serve as a reservoir, especially at the summit of the venous cone, in the auricle. For this purpose, the veins are sometimes developed in the form of plexus, and this arrangement increases their capacity as a whole; these plexus may also be sometimes intended to warm the parts in which they are situated, as we shall see is the case with the choroid plexus (heating apparatus of the retina); but their object is generally to prevent stagnation in the capillaries, and they are therefore arranged and grouped in parts where they will not be subject to compression, as, for instance, behind the body of the vertebræ (between this body and the posterior common ligament.) Moreover, the ramified form and the anastomoses of these plexus prevent any partial and local compression from impeding the return of the circulation, the blood finding always an easy passage through the vessels which have remained open. Finally, there are some veins whose coats are inextensible and incompressible, so that nothing can hinder the circulation in them; and, on the other hand, they cannot swell, so as to compress the adjacent

organs: the *veins of the dura mater* offer the best example of this arrangement.

The veins are generally furnished with *valves*, arranged in such a manner that when any abnormal pressure takes place, they straighten under the influence of the current of blood, which has a tendency to flow back, obliterate the lumen of the vessel, and prevent the blood from returning to the capillaries. These valves thus serve to neutralize, and even to utilize in regard to the circulation, the action of the shock, and of accidental pressure (for instance, on the part of the neighboring muscles, when contracted); they also serve to support, by their division, the long blood columns, as, for example, the venous column of the lower limbs. The veins supporting long columns of this kind have remarkably thick coats; thus the coats of the saphenous veins resemble in appearance those of the arteries, and remain open after incision, in the same manner as the large arterial vessels. Where local pressure is rare, no valves are found in the veins, as in the venous apparatus of the brain and lungs.

As the phenomena of the flow outwards and backwards of the blood through the cardiac orifices gives rise to particular sounds (sounds of the heart, page 140), so the peripheral circulation occasions sonorous phenomena, which may be better observed in pathological cases (anæmia) than in the normal condition, and are heard especially about the neck, no doubt because the aponeuroses of this region, by their special arrangement, cause a state of tension in the coats of the vessels and in their sheath, which is favorable to the transmission of sounds: the tone of these sounds differs very much (whistling sound, musical sound, *bruit de diable*); they are sometimes continuous, and sometimes intermittent; some are produced in the arteries, and others in the veins. Weber supposes them to be caused by the coats of the vessels being made to vibrate by the motion of the blood, — but these sounds are more generally attributed, as is done by Chauveau and Potain, to the blood passing rapidly through a narrow and then through a wider passage, through which it flows more slowly. Chauveau has shown, indeed, that vibrations are produced under these circumstances, by means of a *fluid vein*, which causes a sort of eddy at the point where the narrow part joins the wider (*fluid veins* of Savart). This arrangement may be carried out in different ways; normally, as at the opening of the jugular vein into the subclavian;

accidentally, as by the compression of the vessel by a muscle, by the stretching of an aponeurosis, and, most frequently, simply by the application of the stethoscope. By reproducing these sounds, in glass tubes, Heynsius (of Utrecht) has made the movements of the fluid visible, by means of colored particles in suspension following the eddying and whirling, which become more rapid as the sound is more decided.

It has been also ascertained by these experiments, that fluids of slight density produce sounds more readily than the denser fluids. This fact explains the existence and intensity of the vascular sounds in anæmia and chlorosis; in these cases the quantity of blood globules is diminished, often in such proportion as to lower considerably the density of the blood; we need not, with Peter, look for a spasm of the arterial muscles and the contraction of the vessel, to produce the phenomenon of the fluid vein. Andral's researches have shown that there is always a vascular *souffle* when the number of globules descends below the proportion of 80 to 1000 (eight per cent), and that its intensity depends on the degree of diminution of the globules.

III. Influence of the Nervous System on the Circulation.

We have ascertained the existence of many muscular phenomena in the heart and in the vessels (arteries and veins); this makes it probable that the contraction of these muscles is influenced by the nervous system.

The Heart. — It was however long believed (as by Haller), that the heart is independent of the nervous system, and that the afflux of blood causes the contraction of this hollow muscle, its presence directly exciting the muscular fibre of the cardiac coats. Now, it has been proved beyond dispute, that the movements of the heart as well as the other movements are governed by the nervous system. The spinal cord appears to be the centre of this influence, and we know that any cerebro-spinal shock, or injury to the spinal axis may slacken or accelerate the motion of the heart; this influence may be reflex, and a large number of peripheral impressions may thus hasten or slacken the movement. This is because the spinal cord and the bulb furnish nerves to the heart, the effect of some of which (branches of the great sympathetic) is to quicken its pulsations, while that of others (the pneumo-gastric) is to retard these: thus the pneumo-

gastric is a *paralyzing nerve* of the heart (Weber and Budge). We shall observe similar facts in the innervation of the vessels.

Moderating Nerves of the Heart. — Budge, Weber, and Cl. Bernard (1848) discovered, almost at the same time, that excitation of the entire pneumo-gastric nerve, or of its peripheral extremity only, has the effect of retarding the motion of the heart; thus in the dog, an animal whose heart beats irregularly and very rapidly, such excitation serves to regulate the cardiac pulsation. Different explanations have been given of this phenomenon; some have considered that retardation of the motion of the heart is caused by exhaustion succeeding too violent excitation of the pneumo-gastric nerve: a nerve leading to a muscle could be looked upon only as an exciting agent of this muscle, and the exhaustion of the nerve seemed to explain the retardation which follows excitation. This explanation, however, does not apply to the retardation which follows excitation of the peripheral extremity of a nerve which has been previously cut; and it fails especially when we consider that, by simply cutting the pneumo-gastric nerve, the rapidity of the pulsations of the heart is greatly increased. Since observation of similar phenomena in other parts of the nervous system, has lately made the idea familiar to us of nerves possessing *paralyzing properties*, it is generally admitted that the pneumo-gastric nerve is a moderating nerve of the heart: section of this nerve suppresses the moderating influence, and, consequently renders the pulsation more rapid; excitation increases the moderating influence, and thus retards the pulsation. The theories by which it has been sought to explain the foregoing experiment, while denying the moderating, paralyzing function of the pneumo-gastric nerve, are in many cases extremely complicated, and we will only mention here the facts most recently furnished by experiment. Legros and Onimus, who examined the effects produced by excitation of the pneumo-gastric nerve by intermittent currents of electricity, have shown that, under these conditions, the pulsations become fuller and less frequent in exact proportion to the number of intermissions; the number of intermissions required to produce stoppage of the heart is smaller when the animal is weakened or chilled, or in a state of hibernation. Arloing and Tripier have remarked that excitation of the right pneumo-gastric nerve has more effect on the action of the heart than that of the left. (It should be added that study of the comparative

influence of these two nerves on respiration has induced these authors to allow that the left pneumo-gastric nerve acts especially on the lung.)

Recent investigations by Schiff, however, appear to show that some of the nervous fibres which accelerate the pulsation of the heart, are contained, at least in the dog, in the pneumo-gastric nerve (Schiff, *Lo Sperimentale*, Novembre, 1872.) These fibres appear to come from the accessory nerve of Willis (N. Spinalis), and to join the pneumo-gastric nerve for an instant, quitting it with the superior laryngeal nerve, and reaching the heart after following a most remarkable course, not unlike Galen's anastomosis: (this anastomosis unites the superior laryngeal nerve to the inferior, which also furnishes a cardiac nerve of its own).

Accelerating Nerves of the Heart.—The influence which the cord, by means of the great sympathetic nerve, exercises on the heart, in increasing both the force and number of its pulsations, has been variously explained, and the investigations made on this subject have resulted in the discovery of a nerve whose functions are very peculiar. This is the *nerve of Cyon*, a sensory nerve of the heart; and by means of this the heart produces a reflex action which causes the organs of the peripheral circulation to dilate, and, consequently, enables the heart to diminish the energy and number of its efforts. We borrow from Cl. Bernard's recent lectures (May, 1872), and from his report to the Academy of Sciences on Cyon's experiments, our account of this interesting question.

Le Gallois first pointed out the influence of the spinal cord on the pulsation of the heart. But Von Bezold, by his experiments, in 1863, proved more particularly that section of the cord between the occipital region and the atlas, produces considerable diminution of the pressure of the blood in the large arteries, as well as retardation in the pulsations of the heart. He afterwards proved that excitation of the cord behind this section restores both the pressure of the blood, and the rapidity of the pulsation, thus showing that the effect of the cord upon the heart is to modify the *force* and *number* of pulsations.

Ludwig and Thiry, however, having observed that excitation of the cord, separated from the brain, always exerts its influence on the pressure of the blood, even when the cardiac nerves which unite the heart to the cord have been destroyed, inferred from this that the cord has no real influence upon the heart itself, but upon the peripheral circulating

system; and Ludwig and Cyon proved, by new experiments, that this influence on the peripheral circulating system is principally exercised in vascularizing the abdominal viscera, and is conveyed to them by the medium of the *splanchnic nerves:* by dividing these nerves we obtain effects similar to those which result from section of the cord between the occipital bone and the atlas.

The influence of the cord on the *pressure* of the blood (we are not now speaking of the *number* of pulsations) is as stated by Ludwig; but Cyon has also demonstrated that this influence which is the result of a peripheral vaso-motor modification (see further on, vaso-motors), is by nature reflex, and may therefore be caused by excitation of a sensory nerve, beginning in the heart itself: if, after cutting off this nerve, which is a branch of the pneumo-gastric, its peripheral end be excited, no effect is produced; but excitation of the central end is painful, and causes, when the manometer is applied to the carotid artery, considerable diminution of pressure from a reflex influence bearing especially on the abdominal vascular system (splanchnic nerves), resulting in paralysis and dilatation: in short, the *depressing nerve of the circulation* (of Cyon), represents the centripetal course of a *paralyzing reflex* action, producing depletion of the heart, and, consequently, diminution in the pressure of the blood in general.

Under the influence of these reflex actions, which may also have their starting point in the brain (emotional influences, palpitations, syncope, owing to mental causes), the pulsations of the heart offer the greatest possible variety in number and rhythm, especially in cases of disease. In the normal condition, the average number of pulsations is 72 a minute. This is the average in the adult stage, its minimum being found at the period when growth ceases, and the epiphyses are found united; statistics seem to show that the heart in old age beats faster on the average than in the adult.

In the pathological condition, the changes in the pulsation of the heart, ascertained by the throbbing of the pulse, supply us with valuable information on the subject of the innervation of this organ, but the quickness of the pulse yields no indication as to the state of the circulation, properly so called. If we go back to our study of the mechanism of this phenomenon, we shall understand how the pulse may be quick without the circulation being active; if, for instance, the heart at each contraction sends out more than the usual

quantity of blood. So, at the moment of death, the pulse may be very rapid, while the circulation declines.

The heart, when taken from the body, may still continue to beat: this may be readily observed in the cold-blooded animals, and has also been found to be the case in man; we have found rhythmical contractions still existing in the heart of an executed criminal an hour after death. This is, however, only another reflex phenomenon, the centre for which is found in small ganglions disseminated throughout the substance of the coats of the heart, principally in the auricles and the auriculo-ventricular zones, or, at all events, near the base of the heart. If the heart of a frog be cut in fragments, we find that only those parts of the ventricle or of the auricles which adhere to the base continue to palpitate.

The position of these ganglions, or small reflex centres, found in the heart itself, has been ascertained up to a certain point: there are three principal ones, — *ganglion of Remak*, at the opening of the lower vena cava; *ganglion of Bidder*, situated in the left auriculo-ventricular septum; and *ganglion of Ludwig*, in the inter-auricular septum.

These three ganglions do not all appear to have the same function: the two former appear to be centres of excitation, and the latter of moderation. If the heart be cut into two unequal parts, one containing Remak's ganglion, and the other those of Bidder and Ludwig, the first will continue to palpitate, while the other remains quiet. If then the auricles in this latter part be separated from the ventricle, they will remain in repose, while the ventricle again begins to throb. Thus we see that each of the outer ganglions (Remak's and Bidder's) cause movements which the inner ganglion (Ludwig's) paralyzes, when taken in connection with only one of the two first; but when the heart is entire, Ludwig's ganglion is unable to counterbalance the amount of motor-power of the other two.

The starting-point for these reflex actions is the excitation produced by the presence of the blood on the sensory (or centripetal) fibres in the endocardium, and not directly on the muscular fibre itself. A substitute for this physiological excitant may be found, in experiments, by excitations directed to any point of the heart, particularly the endocardium. If the contact of the blood with the endocardium be prevented the heart ceases its pulsations, the physiological cause of the reflex action being thus removed. If, for instance, the chest, and consequently, the heart, be forcibly

compressed by a strong expiration, so as to empty it completely, and bring its coats into close contact, we may succeed in stopping the beating of the heart. This explains those curious instances of persons who are able at will, to stop the motion, and consequently, the pulsation of their heart. (See *respiration.*)

Vessels. — The vessels which we know contract under direct excitation (heat, cold, shock, etc.), are also, in this respect under the control of the nervous system. Cl. Bernard has demonstrated that effects of this kind belong especially to the province of the *great sympathetic* (vaso-motor nerve), which sometimes produces contraction and sometimes paralysis of the muscular coats of the vessels. Some of the cerebro-spinal nerves produce the same effect. Thus the chorda tympani paralyzes the arteries of the sub-maxillary gland. These phenomena of contraction or dilatation of the vessels have great influence on the calorification of the organs in which they take place: they are for the most part of a reflex nature, and are the consequence either of an impression made upon sensory nerves, or of some mental excitement (redness or paleness of the face under the influence of the passions). The innervation of the vessels thus offers the closest resemblance to that of the heart.

The physiology of the great sympathetic as a vaso-motor nerve offers great difficulties, not only in this general point of view, but also in that of its influence on the vessels, the origin of its nerve filaments, and of their course and relation to the nerves concerned in the organic processes or functions (*vie de relation*, organic life).

After Henle had discovered smooth muscular elements in the coats of the arteries, Stilling found nerves which disappear in these coats, and gave these the name of vaso-motor nerves, seeking to complete the anatomical fact by a physiological hypothesis. Physiological researches on the subject, however, only date as far back as 1851, when Cl. Bernard showed that section of the great sympathetic nerve in the neck of a rabbit produces considerable increase of temperature in the ear of the corresponding side; though at first tempted to ascribe this phenomenon merely to a calorific and direct action of the nerves, he soon saw that the heat of the ear was simply due to a dilatation of the blood-vessel, and to a greater afflux of blood; and showed, simultaneously with Brown-Séquard, that by galvanizing the cephalic ex-

tremity of the cervical sympathetic nerve, when cut off, a constriction of the auricular vessels occurs, and consequently, a return to the normal temperature, or even, from anæmia, a lower temperature may follow.

Since that time, the function (*rôle*) of the great sympathetic, as a vaso-motor nerve, has been clearly demonstrated in other parts of the body, the limbs, and the abdominal viscera, as well as of the head. Kussmaul and Tenner confirmed the opinion that the calorific influence is entirely vaso-motor, and Van der Beke Callenfels (1856) proved that this afflux of blood in any part of the periphery which is much exposed to radiation causes considerable loss of heat in the animal.

Experimental physiology of the great sympathetic as a vaso-motor nerve, may now be pursued by studying the effects produced by its section and excitation, as has been done by Mons. Legros in his monograph: 1. Section of a sympathetic branch is instantly followed by the paralyzation of the smooth muscles innervated by this branch, especially the muscles of the vessels: the small vessels are seen to dilate, and the capillary network to fill, on account of the increased afflux of blood. Generally it may be easily observed in a rabbit's ear, for instance, that vessels which were hardly visible before the operation, can be distinctly seen after it. In short, passive hyperæmia takes place. 2. By bringing an induced current of electricity to bear upon the peripheric extremity of the sympathetic nerve, after section, quite a contrary phenomenon is produced: the vascular muscles contract, the vessels shrink, and active anæmia follows. If the excitation ceases, a marked dilatation succeeds. The capillaries are entirely passive during all these phenomena: the whole process takes place in the small veins and arteries. The essentially passive part played by the capillaries, during the alternations of contraction and relaxation going on in the vessels, is best understood by studying the pressure or vascular tension which accompanies experiments on the vaso-motor nerves. If, indeed, the capillaries dilated, as do the arteries, after section of the sympathetic nerve, the flow of blood would be increased, but the resistance would be less, and the pressure lower. On the other hand, if excitation of the sympathetic nerve caused the capillaries to contract as do the other vessels, the resistance would in-

[1] Ch. Legros, "Des nerfs vaso-moteurs." Paris, 1873.

crease, and the tension of the blood also. Now, what takes place is precisely the contrary; Cl. Bernard has shown by the aid of the differential manometer, that the tension is increased in the first instance, and diminished in the second (Legros).

But how does the great sympathetic nerve act? How does it happen that (during the condition of inactivity) it keeps the vascular coats in a continued state of contraction? How is it that, at certain moments, by means of reflex actions, this nerve causes nearly similar phenomena to those which it exhibits when cut; such as dilatation of the vessels, and greater afflux of blood in certain parts of the organism (sudden redness of the face, turgescence of the erectile tissues, hyperæmia, more abundant secretion of the glands, etc.)?

In replying to the first question *a constant state of excitation of the vaso-motor nerves* is generally admitted: this being due to a continuous reflex action originating in the sensitive nerves of the arteries (Audiffrent) in other sensitive parts; thus the *muscular tonus* has been looked upon as a reflex influence: according to Brondgeest, the *tonus* may be made to cease instantly by section of the sensory nerves proceeding from any part which may be in a tonic condition. According to other physiologists, the constant excitation of the vaso-motor centre is produced by the presence of carbonic acid in the blood. If animals be poisoned by means of this acid, all the small arteries will be found in a contracted state (Thiry).

The second question is still more difficult to answer. It has been clearly demonstrated that repeated excitations produce dilatation of the vessels by reflex action; if the ear of a rabbit be cut off, and the sciatic nerve excited, we see that the blood flows in much greater abundance through the vessels which have been cut. Again, there are centrifugal nerves, irritation of which causes instant dilatation of the vessels; thus the chorda tympani, if irritated, produces severe hyperæmia, and consequently, abundant secretion in the sub-maxillary gland.

It is difficult to allow the existence of nerves which directly paralyze the muscular elements of the arterial tunics; for instance, the chorda tympani, which is a branch of the facial nerve, reminds us rather of those nerves which, by their influence upon others, cause all action to cease in the latter, by a sort of nervous *interference*, as the intervention

of light produces darkness by joining light to light. Claude Bernard appears to have adopted this hypothesis, and it may also serve to explain the nervous mechanism of the afflux of blood in erection: the nerves coming from the cord act upon the threads of the great sympathetic nerve so as to prevent their action, causing turgescence and hyperæmia of the erectile tissue. Section of the cord does not cause continuous erection, because the nervous influx of the spinal (rachidian) nerves can no longer act upon the sympathetic nerves, and this association of nervous influences is alone capable of producing vaso-motor paralysis. In adopting this hypothesis, the influence of the first nerve on the second must be considered as equivalent to the section of the great sympathetic nerve made by an operator who desires, for instance, to produce hyperæmia of a rabbit's ear.

This view, however, does not satisfy all who have made the experiment, because some among them have been convinced that more serious hyperæmia takes place under the influence of reflex phenomena in a less degree than any which may be caused by section of the great sympathetic nerve in the same parts: the idea has thus been suggested of *active hyperæmia*, more intense than *passive* or *paralytic hyperæmia*, and two theories have lately been formed on this subject; that of Schiff, or *active dilatation of the vessels;* that of Legros and Onimus, or *peristaltism of the vessels.*

This theory of the *active dilatation* of the vessels was for a short time entertained by Cl. Bernard, but he now appears to have finally renounced it: it is not easy to prove it by anatomy, for it supposes the existence of longitudinal muscular fibres in the coats of the arteries, and of these histology shows no trace. Schiff, therefore, carefully abstains ("*Leçons sur la Physiologie de la Digestion*") from stating his theory in explicit terms; he still regards as inexplicable both the origin and the mode of action of these dilating nerves, but he relates many experiments, which, to his view, make their existence undeniable.

He observed, in the small arteries of a rabbit's ear, phenomena of systole and diastole, appearing from 2 to 8 times in a minute (this by no means coincides with the beating of the heart). These movements cannot be the consequence of alternate contractions of the veins, for direct inspection of these vessels reveals nothing of the kind; neither are they caused by paralysis of the arteries succeeding to a momen-

tary contraction for the diastole observed in the uninjured animal is much greater than can be produced by section of the great sympathetic nerve, in other words, by paralytic dilatation. The diastole observed would be then really an *active dilatation.*

Irritation of the central extremity of the auriculo-cervical nerve (auricular branch of the cervical plexus) produces, by a reflexive course, dilatation of the vessels of the ear; this the same experiments prove to be an essentially active, not paralytic phenomenon (there is no contraction of the veins, — paralytic dilatation).

Vaso-motor reflexes (reflex actions) of a similarly active nature, and more powerful in effect than the paralyzing influences, have been observed by Schiff, by placing the animal (dog or rabbit) in a vapor-bath, or producing in it a septic fever, exciting its passions, etc.

Finally, Schiff ascertained that irritation of the peripheral extremity of the auricular branch of the trifacial immediately produces these active dilations; one of these nerves, like the chorda tympani, acting upon these organs in such a manner as to produce in them *functional hyperæmia*, which Schiff prefers to distinguish from *neuro-paralytic hyperæmia*, without, however, denying the existence and importance of the latter.

The theory of the *peristaltism of the arteries* is more complete; it seeks to explain normal as well as pathological facts, and enters into the closest details of the question. Legros and Onimus ground this theory on investigations of three kinds: —

1. Direct inspection of the small arteries discloses *vermicular* or *peristaltic contractions*, beginning in the principal trunks, extending to the smallest arteries, and assisting the progress of the blood. Goltz and Thiry had already ascribed to a similar mechanism the evacuation of the arteries after death. Onimus observed these movements in the vessels of the inferior animals (annelida), in which their existence had long been recognized, but he has besides pointed them out in the interdigital membrane in frogs, and even in man in the small arteries of the eye: "if the central artery of the retina be obstructed by a clot, we see, by the aid of the ophthalmoscope, that the small arteries, which show the existence of a collateral circulation, have very marked peristaltic movements."

2. On modifying or suppressing the action of the heart, we find that the blood still circulates in the arteries, and flows into the veins, and, under these circumstances, an injection made upon a dying animal is most likely to succeed, the peristaltism of the arteries making the blood penetrate the finest nets of the capillaries. The weakening of the heart by the administration of chloroform, of digitalis, or of alcohol, in an animal in whom the cervical portion of the great sympathetic is cut on one side, produces an excess of temperature, not of the side operated upon, but of the other side; the peristaltism of the arteries on this side alone being capable of producing a *hyperæmia*, which may be called *active*, but must not be confounded with the active dilatation of Schiff.

3. By applying irritants to the peripheral extremity of the sympathetic nerve when cut, we produce very different results, according as the excitations produced are tetanic, or calculated to bring the peristaltism of the arterial tunics into play. Thus, while powerful excitants produce anæmia of a rabbit's ear, by producing a state of energetic and permanent contraction, we find, on the contrary, that a slight ligature, or the action of glycerine, or of nitrate of silver, etc., causes considerable hyperæmia, more important even than passive hyperæmia (neuro-paralytic); these results are, however, still more striking if electricity be employed. While interrupted currents (faradaic) paralyze the arteries (causing anæmia), we find that the continuous current (and only when its direction is centrifugal) produces a very considerable hyperæmia in parts to which the sympathetic nerve, which is thus excited, is distributed. Under similar circumstances, microscopical examination of the interdigital membrane of a frog reveals very decided peristaltism of the small vessels, during the passage of the centrifugal continuous current.

Thus certain excitants produce in the arteries slight or clonic contractions, causing peristaltism and subsequent hyperæmia. Others cause tetanic contractions, bringing on anæmia and chill.

Differences of the same kind are observed in the manner in which physiological excitants, the passions, for instance, act on the vascularity of the skin in general, and on that of the face in particular. Moleschott, who was attached to the theory of vaso-motor paralyses, had already divided the passions into *paralyzing* and *exciting passions;* but when we see, for instance, a slight anger cause redness of the face (red anger) and a greater access of the same passion produce

paleness (white anger), is it not more reasonable, instead of maintaining that a low degree of this passion is paralyzing and a paroxysm exciting, to see in the first case a slight, clonic excitation, causing peristaltism and hyperæmia; and in the second a violent tetanic excitation, producing permanent constriction of the vessels, anæmia and extreme paleness?

We see, by the statement of these different and, often, opposing theories, that we are still far from being decided as to the nature of the vaso-motor phenomena, or *vasculo-motors* (Béclard). More just ideas, up to a certain point, have been acquired on the *origin* and *course* of the vaso-motor nerve fibres.

The *vaso-motor centres* are placed, partly in the spinal cord, but principally in the cephalic (cerebral) parts of the medullary cord, for section of the cervical cord causes dilatation of all the arteries of the body. Experiments by Ludwig, Thiry, and Schiff, show that these centres are placed in the protuberance and peduncles of the brain: here take place the central phenomena of reflexes which, after irritation of the sensitive nerves, diminish the tonicity of the vessels. Injury to the cerebral peduncles causes hyperæmia, especially in the abdominal viscera, and may lead to softening of the gastric mucous membrane or coat (Schiff). Irritation of these peduncles causes retraction of all the vessels (Budge). The cerebellum appears, however, to have some share in the vaso-motor operations, and the cervical cord may be the seat of the vaso-motor phenomena concerned in the functions of salivary secretion.

From these vaso-motor centres originate centrifugal fibres, following the spinal axis, and passing successively to the arteries by the medium of the great sympathetic nerve. In this course the vaso-motor nerves follow especially the antero-lateral columns: they cross each other, for, in hemiplegia from a central cause the vaso-motor lesion, as with other lesions of the motor tract, is observed on the opposite side to that of the encephalic lesion; this decussation, however, as with the voluntary motor nerves, appears to be made suddenly at the level of the bulb, and there is no other decussation of the vaso-motor nerves in the remainder of the spinal axis (Brown-Séquard). Thus, in spinal hemiplegia, the vaso-motor disturbances are observed, like those of the motor tract, on the same side as the medullary disease, and on the opposite side to the disturbances affecting sensation (see page 46): that is, the

paralyzed member is, on account of the dilatation of its vessels, warmer than the sound member; but continued motion, and consequently, greater intensity of combustion, in the latter, may cause a difference of temperature in the opposite direction; and in this manner must be explained those contradictory results of observations which have suggested to V. Bézold the idea that the vaso-motor nerves of the inferior extremities remain on the same side of the spinal cord, while those of the anterior extremity are interlaced along the medullary cord; while Schiff has formed the still more singular hypothesis that the course of the vaso-motors of the leg, the foot, the hand, and the forearm, is direct; whilst those of the pelvis, the thigh, the arm, and the shoulder, are crossed.

The vaso-motors spring from the cord by the anterior roots of the spinal nerves. This fact has been put almost beyond the reach of doubt by Claude Bernard's investigations of the vaso-motors of the thoracic portion of those which control the secretion of the saliva, and finally, of those sympathetic branches which, without being exactly vaso-motors, bear the closest relationship to these nerves. We mean those filaments which control the oculo-pupillary phenomena, which are observed to take place after section of the cervical sympathetic cord (contraction of the pupil, sinking of the eyeball, etc.).

What is remarkable, though, is that the height of the roots from which the vaso-motors spring does not at all correspond to the height of the organs or of those parts in which these nerves are distributed: thus Cl. Bernard has demonstrated that the vaso-motors which join the brachial plexus, and then proceed to the thoracic portion, come to it by the ascending filaments of the thoracic cord of the great sympathetic nerve, those which join the sciatic nerve coming by the descending filaments of the lumbar region cord; they thus emerge from the spinal cord: the former from much lower, and the latter from much higher, roots than those of the corresponding nerves to which they are afterwards united. The oculo-pupillary sympathetic branches, finally, spring from the spinal cord, by the roots of the first two dorsal pairs, in a manner quite independent of the corresponding vaso-motors. We see thus, that the study of the passage of these nerves offers unexpected complications, and difficulties which it is not easy to remove by experiment, their course,

according to Schiff, differing in animals of the same kind, under different circumstances.

As the vaso-motors spread into the arteries, they follow an independent course in certain parts, as in the neck and head, where the sympathetic nerve, even in its secondary plexus, is detached from the nervous system which presides over the organic processes; in other cases, their arrangement exactly resembles that of the arterial branches (abdominal sympathetic); or, finally, as is the case with the limbs, they unite and are lost in the nerves of the brachial and lumbar plexus, etc., the union being made at the level of, or at a certain distance from, the plexus; in the case of the sciatic nerve, a little before it leaves the pelvis, and in the nerves of the arm, at the level of the brachial plexus (Claude Bernard).

The modifications caused in the circulation by the functions of the vaso-motor nerves, are extremely important when considered in reference to the phenomenon of *secretion* and *calorification* (see *animal heat*, farther on). These modifications should be also closely studied in regard to many pathological phenomena. Thus *fever* is owing, in a great measure, to a derangement of the vaso-motor nerves paralyzing the vessels, and producing a change in the regulation of the heat of the body. A remarkable disagreement may also sometimes be observed between a local disease and the fever which accompanies it. The latter may break out, or cease suddenly, by a modification which is in some respects dynamic (nervous system), while the disease must run its course through all the phases of cellular and vegetative growth (Hirtz).

In order to complete the history of the vaso-motor nerves, it would, finally, be necessary to review the numerous therapeutical applications by which these modifications may be produced, but we will mention one only of this class of medicaments, — *digitalis;* this substance has the effect of lowering the pulse and diminishing heat, and is, therefore, a powerful agent against fever, the pathological physiology of which may be briefly stated in these few words. Besides retarding and regulating the motion of the heart, digitalis also acts on the peripheral organs of the circulation, causing contraction of the coats of the arteries, by exciting the vaso-motor nerves (Ackerman). When slackened by digitalis, the pulse becomes stronger and fuller. The tension of the arteries appears to increase, and the special power of this

remedy seems to consist in its restoring the contractility of the small arteries under the influence of the vaso-motor nerves proceeding from the great sympathetic. Digitalis must, therefore, be henceforward considered as regulating the circulation by means of an exciting, tonic action, and not a hyposthenisant as is generally supposed (Hirtz, "Nouv. Dict. de Méd. et de Chirurgie").

IV. General Uses of the Circulation.

The principal purpose of the circulation is to produce rapid currents in the interior of the tissues, intended to supply the organs with the materials of nutrition, and to carry off the waste resulting from the changes which these undergo, as we pointed out at the beginning of our description of the organism. These changes take place in the capillaries; we know that the pressure in these small vessels is generally from $\frac{10}{100}$ to $\frac{12}{100}$ of the atmosphere, and this pressure appears very favorable to the regularity of the changes. When the pressure is diminished, as after bleeding, reabsorption takes place; if, on the contrary, the pressure in the capillaries is increased, as by compression or ligature of a vein, the exudation exceeds the normal limits, and the serum of the blood, overflowing into the tissues, constitutes what is called *œdema*. Paralytic dilatation of the small arteries may also produce œdema by increasing the afflux of blood, and, consequently, the pressure in the capillaries.[1] The stings of

[1] According to a recent communication by Ranvier to the Académie des Sciences (January, 1870), vaso-motor paralysis is the most important condition in the production of œdema. In attempting to produce artificial œdema by compression and obliteration of the veins, Ranvier was surprised to find that the ligature never caused serous infiltration in the parts situated beyond it.

In experimenting on rabbits and dogs, he tied, first, the two jugular veins at the base of the neck; second, the femoral vein, at the level of the crural ring; third, the inferior vena cava. In none of these cases did œdema ensue, either in the face or the lower limbs; while, having cut the sciatic nerve on one side, thus paralyzing the vaso-motor nerves of the limb, in a dog in which he had tied the inferior vena cava, he found that considerable œdema followed on this side, and the other remained in its normal condition. The same phenomenon was repeated in several experiments.

It is true that the sciatic nerve is a mixed nerve, containing in the same covering sensitive fibres, voluntary motor fibres, and vaso-

insects or of venomous plants (the nettle), produce by this mechanism the rapid swelling by which they are distinguished. Beside the influences of changes of pressure, we must also take into account the physiological properties of the globules in the vicinity of these vessels, for we know already, and shall soon see more particularly (study of the epithelial or mucous and glandular surfaces), that there are certain tissues formed of globules which act as barriers to the passage of fluids while others more especially assist; in other words, the tissues near the capillaries exercise more or less attraction to the contents of these tissues.

Beside these general functions, the circulatory system exhibits special arrangements in certain parts, indicating some special and accessary purpose; thus the vessels, in some organs, have to perform the part of supplying heat as well as nutrition, as the vessels of the external ear, of the face in general, the extremities of the fingers, and the integuments of the articulating regions; these vessels are much more numerous in all these parts than the simple purpose of nutrition requires. In other parts the capillaries are arranged with a special view to absorption or exhalation, as those of the lung, which form in this viscus a large work of blood-vessels in which the red globules become impregnated with oxygen, while the serum evolves its carbonic acid.

The afflux of the blood has also a mechanical part to play, that of erection, for instance; it is in this case only, that we find those *accessary peripheral hearts*, intended to increase the tension of the blood in the organs which are capable of erection: by their rhythmical contraction during erection, the bulbo-cavernous and the ischio-cavernous muscles drive to the extremity of the penis the blood which has flowed into the bulb of the urethra, and the root of the cavernous bodies.

The movement of the circulation is indispensable in order to keep the blood in its physiological condition, a fluid state; not that the motion prevents the coagulation of the blood; on the contrary, it promotes it, and it is by beating that the

motor fibres. But Ranvier had satisfied himself, by previous experiments in tying the inferior vena cava, that destruction of the sensitive roots and of the voluntary motor roots at their issue from the spinal cord was followed by no œdematous phenomenon in the abdominal region. Paralysis of the vaso-motor nerves appears thus to be the cause of the dropsy which takes possession of the limb which has undergone section of the sciatic nerve.

fibrine is extracted from the blood; but the movement of the circulation brings the different parts of the mass of blood into continual contact with the inner coat, the *endothelium* of the vessels. Among the more or less well-defined causes already mentioned (page 125), influencing the coagulation of the blood, the least disputed, though most difficult to explain, is the still puzzling influence of the *inner coat of the living vessels*. This influence was pointed out by Brücke: *contact with the living coat is a powerful obstacle to coagulation;* the fibrine cannot become solid, while the blood is circulating, and while each of its particles comes constantly in contact with the living coat.

As soon as the circulation ceases, the central layers of the blood current have a tendency to coagulate: examination of the manner in which this coagulation is produced, constitutes the study of clots formed *after death*, and is no less important to the physiologist than to the pathologist, whom it teaches how to distinguish recent from ancient clots. The blood in a corpse does not directly coagulate when the action of the heart ceases; the mechanism by means of which the dying arteries drive their contents into the veins (see *natural form of the arteries*, page 153), forms still a kind of circulation, preventing this coagulation: in a corpse, therefore, clots are generally found only in the veins.

When the veins of a corpse are gorged with blood, which has poured in from the arterial system, coagulation begins to take place in the central layers, because the most distant from the coat; here the fibrine coagulates rapidly, entangling the red globules in this part of the blood, which explains the fact that the centre of the venous clots is always red or black, in short, appears *cruoric*.

From 20 to 24 hours, at the least, elapse before the most peripheral parts of the contents of the veins are completely coagulated; here the influence of contact with the living coat is still felt. It rarely happens that the death of all the anatomical elements coincides with the general death, the last breath and the last pulsation of the heart; we have seen that the muscles and the nerves continue excitable long after this, and that the epithelium of the bladder still resists the phenomenon of absorption for several hours; we shall find that the vibratory epitheliums continue their movements during from 8 to 10 hours; the case is the same with the *endothelium* of the blood-vessels, and it is only at its complete death, at the end of 20 or 24 hours, that coagulation of

the most peripheral layers of the venous blood has been accomplished: a bloody fluid is often extracted from the vessels of a corpse, already in the state of cadaverie rigidity, which, being placed in a vase in contact with the air soon coagulates, almost like blood taken from a living animal.

Coagulation in the corpse taking place thus slowly, we have here all the conditions favorable to the separation of the fibrine and the globules, and to the formation of a *buffy-coat* (see *buffy-coated blood*, p. 126). The vessels, indeed, may be considered as forming a reservoir of a complicated form, in which during coagulation the fibrine and globules are placed in layers according to their weight, the globules in the inclined parts, the fibrine in those more raised, in the form of *colorless clots:* whence the *mixed clots*, or those formed partly of *cruoric* clots (centre and inclined parts of the coagulated masses) and partly of *discolored* or *buffy-coated* clots. In the latter, as in the buffy-coat formed after coagulation in a vase, are found a large number of white globules (Fig. 55), so many, sometimes, being joined together, that they might easily be taken for a collection of pus.

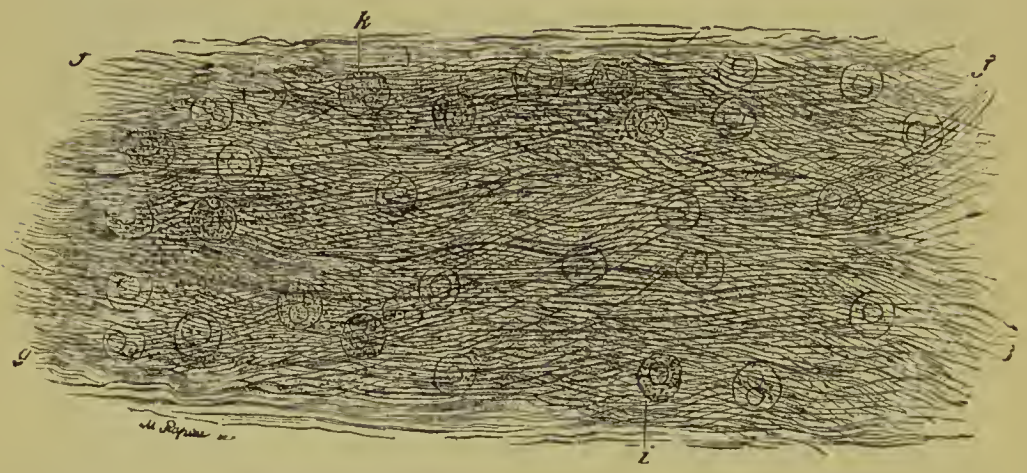


Fig. 55. — Fibrinous clot without red globules.*

The arrangement of these mixed clots is determined by the position of the body after death: thus, the corpse being generally laid upon the back, the clot in the vena cava is colorless in the vicinity of the heart, and becomes darker towards the lumbo-dorsal region, which is more inclined,

* *f, g, j*, Thin fibrinous layer, showing the interlacing of the striæ of the fibrinous layer. *i, k*, Leucocytes united with the fibrine, and bleached by the action of water (500 diam.) (Robin, "Traité du Microscope.")

becoming again colorless in the sacro-vertebral angle, which is a little more raised, and resuming its cruoric appearance in the iliac veins, especially in the inner ones; the clots in the pulmonary veins are always very dark, on account of their inclined position. By turning the corpse over, while these clots are forming, their position is changed, and mixed clots of an opposite composition obtained.

It is plain how useful and important these facts may be, in legal medecine, for instance, by deciding the position in which a corpse has lain during 24 hours after death. They are all the result of that singular property by which the internal coat of the vessels prevents coagulation.

This is not the only property of the vascular walls; it is observed that coagulation in the vessels produces a clot, but little or no serum is found: this is owing to the fact that when the arterial coats lose their properties as living tissues, the fluid part of the blood predominates; either because these coats, being no longer living, cannot effect those natural changes of absorption, etc.; or because the separation of the fibrine has left the other albuminous elements of the blood in a state of composition favorable to their exudation, as occurs in the living body, and, by a similar mechanism, in certain forms of œdema and albuminuria.

PART FIFTH.

EPITHELIAL GLOBULES AND EPITHELIAL SURFACES IN GENERAL.

We have studied the nerve globule, which by its prolongations places the globular elements of the organism, or of their derivatives, in relation with each other (reflexes); and the muscle, which, obeying the motor prolongations of the nerve globule, serves to modify mechanically the relations between the different parts of the organism to each other, or to the outer world; we have seen that, for this purpose, there are numerous mechanical apparatus attached to the muscle (bones, tendons, ligaments, etc.); we have, finally, studied the blood globule, and the blood, which, loaded with the new materials absorbed by certain surfaces of the organism, carries these former into the deeper tissues, while it draws to the excretory surfaces the products of decomposition and of the interior combustion of the organism. We have now, therefore, to study the physiology of these surfaces, that is, the epithelial globules.

Anatomically speaking, the epithelial globule is already known to us; what especially distinguishes it is its relation to the free surfaces of the body; its surfaces are, in fact, formed of membranes, composed of a more or less close padding of connective and elastic fibres, and are covered by an element of which modern anatomy alone has conceived the importance, — epithelium.

It was long believed that the first organ which appears in the embryo, is the nervous system. Modern histological research has proved that the first layer of blastoderm is of an epithelial nature: this layer, in its subsequent development, becomes the intestinal epithelium, the first organic membrane which distinguishes the individual. The importance of the

epithelium, particularly that of the digestive organs, is thus shown by its early formation; its dimensions, in the embryo, are immense. We find that, by the thickness of its layers, it blocks up the opening of the small intestine in the fœtus, and even in the adult it is sometimes 4 or 5 times thicker than the membrane which supports it.

I. General Anatomy of the Epitheliums.

Anatomists recognize two distinct forms of epithelium, *pavement* and *columnar epithelium;* it is only in their extremes, however, that they differ so much, there being intermediate forms between them. The principal epithelium, for instance, that which forms the essential parenchyma of the glands, is neither the pavement nor the columnar epithelium; it is a kind of spherical globule.

The membranes, whose free surface is coated with epithelium, belong to two categories: 1, *serous membrane*, generally forming closed cavities; 2, *integumentary membrane* (either *internal* or *external*). The distinguishing characteristics observed in these membranes are dependent on the nature of their epithelium.

A. *Serous Membrane.*

The class of epithelium spread on the surface of the serous membranes, is the pavement form (Fig. 56, A). It is generally a single layer of cells which, in consequence of reciprocal deformation (being crowded together), have flattened into angular, polygonal disks: such is the epithelium of the abdominal serum; the case is the same with that of the pericardium, of the arachnoid membranes, and of all the serous membranes called visceral. The epithelium which lines the inner surface of the blood-vessels, and the cavities of the heart (endocardium) is also of this kind. The epithelium covering the articulating cavities is also pavement, but composed of several layers;

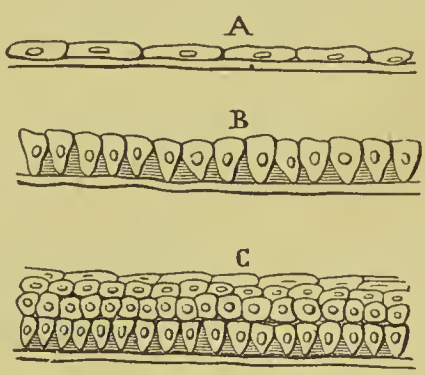


Fig. 56.
Various forms of epitheliums.*

* A, Pavement epithelium. B, Columnar epithelium. C, Stratified epithelium.

there are, beside, gaps in this epithelial casing (synovial), where the cartilages come into contact, and where there is, consequently, the strongest pressure. The opinion can no longer be held that the fibrous substratum of the serous membrane alone ceases to occur at the level of the articulating cartilages, while a layer of epithelium remains on these articulating (cartilaginous) surfaces. The articulating surfaces are closed cavities, but their whole inner surface is not lined with epithelium.

B. *Integumentary Membranes.*

Many organisms possess only one external integument; this is the case with vegetables. But animals, under their cutaneous surfaces, have internal surfaces, communicating with the exterior; these are *mucous membranes.*

a. External Integuments. — The epithelium of these surfaces is composed of numerous layers: on the surface are found flattened cells, while globular forms prevail in the deeper layers; these latter elements exhibit those signs of life which characterize the epitheliums; in fact, what is commonly called epidermis, the most superficial layer of the skin, is not living epithelium, but a dead body, a horny substance as impermeable as India-rubber. But below, is found a soft succulent membrane, which has all the features of the epitheliums of the mucous membranes, and was formerly called *Malpighi's net* (*rete malpighianum*); this, properly speaking, constitutes the living epidermis: it forms a continuous covering to the surface of the dermis.

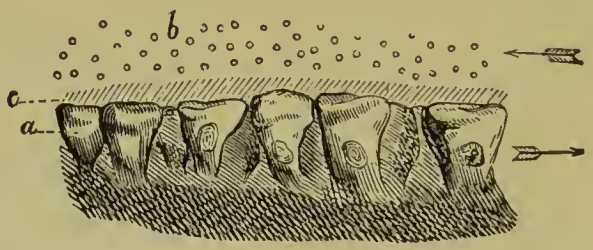


Fig. 57. — Columnar epithelium, with vibratory cilia.*

b. Internal or mucous Integuments. — All the sub-diaphragmatic part of the intestinal canal, the beginning of the trachea and of the genital organs, and their course as far as

* *a*, Body of the cells. *c*, Cilia. *b*, Molecules floating in the ambient fluid, and driven by the cilia in the direction of the upper arrow, in which direction they are erect, while in that of the lower arrow they appear bent. (Valentin.)

the internal genital organs, properly so called, exhibit the features of the external integuments, if the essential element of the mucous membrane, epithelium, be taken into account; the *pavement* form being always found on the surface, and the *globular* forms beneath. But if we penetrate these organs more deeply, we find that the epithelium changes its form, and becomes cylindrical. Thus, in the epithelium which covers the uterus, the spermatic organs, the stomach, the intestine, and the trachea below the vocal cords, we recognize certain general features, such as the cylindrical or conical form of cells, and the constant presence of the nuclei (Fig. 58); and also, characteristic peculiarities, of which the most important is the existence in some of them of *ciliated prolongations*, with which their free surfaces are provided, having a continual vibratory movement, which lasts all through life: this movement is apparent, even some time after the death of the general organism (cessation of the circulation and innervation) these are the *vibratile columnar epitheliums* (Fig. 57).



Fig. 58. — Columnar or cylindrical cells of the intestinal mucous membrane. (Robin.)

The movements of the vibratile cilia of the cells are among the most curious phenomena presented by the epitheliums: the movement of the free cells, furnished in some cases with several cilia which assist them in locomotion, are of the same kind; we shall see further on that the spermatozoids are elements of this class; these elements become more numerous as we descend the scale, until, at length, we find them representing organisms which are endowed with a perfect individuality.

The cells having vibratile cilia are always cylindrical in the higher animals: in the mollusks and in beings of a still lower order, they appear under every possible form. It is remarkable that no epithelium with vibratile cilia has been observed among the articulata (insects). The cilia which spring from the base of the cells are generally fine and straight, but they are sometimes so bulky and their motion so extended, that the glittering waves which they produce on the surface of the mucus may be seen with the naked eye, as on the branchial lamellæ of the mollusks. On examining these movements with a powerful magnifying lens, we find that the cilia either bend in the shape of a hook, or perform

a circumductory movement in such a manner as to describe a sort of funnel, or else curve like a whip-lash (*flagellum* of the infusoria, tail of the spermatozoids), or simply oscillate, however, always more towards one side than the other, so as to produce, at length, in the fluid or mucus in which they are immersed, a progressive movement which is always in the same direction (Fig. 57, upper arrow). Their rapidity of motion renders observation of them often extremely difficult, as they make, at times, from 200 to 250 movements in a second.

When examined with a less powerful magnifier, the result of these movements gives the epithelial surface in which they take place the aspect of a field of wheat moved by the wind, or of a river glistening in the sun. Small bodies (coal-dust), placed on this surface, move upon it in a decided direction. These phenomena may be easily observed in the frog: in the mucous of its trachea the motion is seen to proceed from the lower to the upper part, that is, from the lung to the mouth; in the pharyngeal and œsophageal mucous, on the contrary, it proceeds from the mouth to the stomach. These currents are explained by the fact that the vibrations of these filaments are made in a peristaltic form; that is, in those of the œsophagus, for instance (in the frog), the movement or undulating wave begins in the cilia of the cells of the tongue, and continues in those which are situated lower in the pharyngeal duct; the nervous system, meanwhile, has nothing to do with the *co-ordination* of these movements, and on a piece of detached mucous we may by the regular direction of the movement even distinguish the buccal extremity from the œsophageal extremity of the fragment; we see the cilia, also, fall and rise ten or twelve times in a second, and, like oars, hold out their thin edge as they rise, and strike with their flat surface as they sink, by which means they advance. (The process may be reversed, according to the peculiarity of the animal under consideration.)

If the surface be scraped, and the cells detached from it, we find that the cilia with which they are still provided, continue to move, but in an irregular manner: while the cell floating in the fluid, being displaced by the movements of the cilia, eddies about at random. Michael Forster compares it, under these circumstances, to "a boat without a rudder, manned by mad sailors." It is thus probable that, when the cells are in their accustomed place, the movements of the vibratile cilia (those of the mouth in their relation to

those of the pharynx in the frog), by their contact cause those next to them to enter into action; and thus, by the mechanism of constantly succeeding impulses, this wonderful chain of influences is produced.

If, however, the cilia be detached from the cell to which they belong, they immediately cease to move: their life is, thus, evidently bound up with that of the cell, and especially of the protoplasm filling the cell of which they form a part; Eberth and Marchi, indeed, have discovered that, in the mollusks, the vibratory cilia penetrate the plane with which the free base of the cell is furnished, and come in close contact with the cellular contents; and, by means of the modifications which the vibratile cilia undergo at the beginning of a coryza, Ranvier has shown that this important feature of structure is found in man also.

Different circumstances tend to modify the vibratile movements of these epitheliums: they have been studied with great minuteness by Michael Forster and by Calliburcès in the œsophagus of the frog. They are checked by anæsthetics (ether, chloroform), but regain their vivacity on withdrawal of the vapor; according to Michael Forster, the absence of oxygen appears to paralyze them as if by producing a state of asphyxia. Acids render them immovable, but alter their structure; the movements may, however, be resumed, if the acid be much diluted and neutralized by an alkaline solution; these alkaline solutions are very effectual in accelerating the motion (acids and alkalies produce an exactly similar effect upon the spermatozoids). A low temperature slackens their motion, whilst a high one increases it; in the hibernating animals the movements appear to cease during hibernation (?). No poison has any effect upon them, unless the animal be poisoned, or the poisonous substance placed directly on the epithelial surface.[1]

[1] A curious fact has been brought to the notice of the American editor. The American black bear, which is a good illustration of a hibernating animal, cannot eat food in winter with impunity. Two bears were kept during one winter under observation. As in their natural abode they went to sleep on the first appearance of cold weather. Two or three times they were easily aroused from their sleep, and during one of these occasions one of them was induced to take a very small portion of simple food. During the next two or three days, though asleep most of the time, it sickened and died. The other bear, who was not allowed to be disturbed until the opening of spring, recovered his activity; but,

These epitheliums with vibratile cilia, which were first studied in the lower animals by Hunter Sharpey and Ehrenberg, have been since discovered in different mucous coverings of the vertebrated animals, and the mammifera. In the adult man they are found in the nasal fossæ, the trachea, the large bronchi, the eustachian tube, the membrana tympani (the inner surface of the tympanic membrane excepted) the nasal canal, the deferent canals, the canal of the epididymis, and the canals of the seminiferous cones; also in the Fallopian tube and the uterus in woman. (Fig. 59.) In the fœtus they are also found in the canal of the spinal cord, and the cerebral ventricles which follow it.

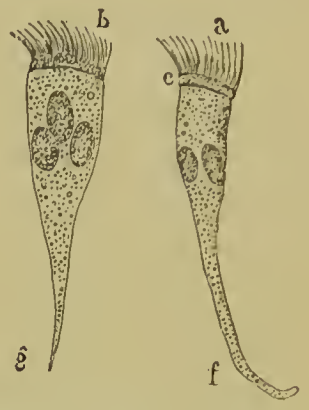


Fig. 59. — Cells of the uterus hypertrophied, and with the multiple nuclei. — Robin, "Anatomie et Physiologie Cellulaires."

In the other vertebrated animals the epitheliums are more widely diffused, becoming still more numerous in the non-vertebrated animals (the mollusks especially), in which they sometimes line the whole external integument and the mucous membrane of the digestive tract.

II. General Physiology of the Epitheliums. — Lymphatic System.

A. *The epitheliums preside over the interchanges of nutrition at their free surfaces.*

We have already seen in our general sketch of the organism that the epitheliums manage the phenomena of interchanges with the outside, and that, in this respect, they are divided into three classes: those which are impermeable, and offer no passage either from the outside to the inside, or the opposite; those which allow a passage from the exterior to the interior (absorption); and those in which, on the other hand, the passage is from the interior to the exterior (secretion).

contrary to what is generally believed, was not perceptibly thinner than in the autumn. In fact, the New England hunters say that the amount of grease derived from these animals in the month of May is very considerable, even if the preceding winter has been long and severe.

In order to perform these latter functions, the epithelial surfaces extend as far as possible, vegetate, and form projections, for the purpose of absorption; as well as internal *vegetations* or *glands*, for the purpose of increasing the number of secreting elements.

These forms of vegetation may have still another object; the epithelial surfaces being the only points at which the peripheral extremities of the sensitive or centripetal nerves come in contact with the outer world, certain epithelial shoots (papillæ) are intended to increase and facilitate these connections; this is the origin of the organs of the senses. These shoots, whose business it is to perfect sensation, may not only be produced outside, like the papillæ in general, but also in the very depths; and one of the most important parts of the eye, for instance the crystalline, is only a deep budding (*bourgeonnement*) of the epidermis.

We must, therefore, study the internal and external integuments, first in regard to their permeability, that is, absorption and secretion, and then to their sensibility. We will begin with the epithelium of the digestive tube, and of the respiratory apparatus, which are especially appointed to absorb the fluid and gaseous materials, and are the seat of numerous secretions and exhalations. We will then examine the cutaneous surface, whose functions are principally those of secretion and sensibility. Here the organs of the senses will come in, being, for the most part, attached to the cutaneous system (sight, hearing, touch), or to the beginning of the digestive or respiratory organs (taste, smell).

In all the general organs, the functions of the epithelium are most important and essential, but they cannot be performed without the assistance of numerous other organs, whose part is either mechanical (muscles) or nervous (reflex influences).

Nothing shows the importance of the epitheliums so well as a consideration of the part which they play in diseases of the surfaces covered by them. Diseases of the epithelium prevail, in fact, beyond all those of the surface which it covers. For instance, pseudo-membranous inflammation of the respiratory tree consists principally in hypertrophy of the tracheal epithelium, and these croup-membranes are found in numerous transient forms, in which the primitive form may be discovered, proving that they are only impaired or degenerated epithelium. The same fact is observed in the deep-

seated epithelium of this system, the epithelium of the pulmonary vesicles: *pneumonia*, or inflammation of the lungs, is only an alteration of the epithelium of the vesicles; these cavities are often found filled with fragments of epithelium to such an extent that the air is entirely excluded. *Tubercle* is *hypertrophy* followed by a sort of *mummified deposit*, formed by the epithelium. This deposit softens after a time, — a chemical change similar to that observed in the work of the glands.

In the intestinal canal, the pathological condition offers us also some important glimpses into the *rôle* of the epithelium. *Dysentery* is a croupous inflammation of this membrane, its morbid product being degenerated epithelium of the large intestine. An intestinal loop in strangulated hernia also exhibits croupous transformation, and this same epithelium also plays the chief part in degeneration of the mucous coat.

The case is the same with the skin: physiologists for a long time attached no importance to the epidermis, regarding it as a secretory product of the dermis, and yet it is the epidermis which is principally affected in diseases of the skin, and by far the greater number of the diseases called *dermatose* are only *epidermatose*, deterioration of the cutaneous epithelium or *epidermis*. In producing certain dermatoses artificially, we place the germ of the virulent malady which we wish to ingraft, not in the dermis, but on the surface, or in the depths of the epidermis. In these layers, too, the first signs of most cutaneous diseases appear; these are always, at least in the commencement, only degeneration of the normal product. The elements of *epithelial cancerous tumors*, however, are in themselves normal; what renders the product morbid in this case is hypertrophy of these elements, an increase in number and size. The same remark applies to what are called benign tumors, to *corns* and *callosities*, which are all abnormal developments of epidermis; these, meeting with some resistance on the surface, penetrate the interior, breaking through the dermis, the aponeuroses, the tendons, and the muscles, until they reach the bone. Those tumors in the integuments, called *sebaceous wens*, which are at first only as large as the point of a pin, and afterwards often attain considerable size, are also accumulations of epithelial degeneration.

The vitality and importance of the epithelium are not less striking when we examine that which lines the serous mem-

brane; in acute effusion of the peritoneum hypertrophy of the epithelium of the serous membrane takes place, occasioning, exactly as in the case of the mucous, the formation of false membranes; also, chronic effusion, when not produced by mechanical causes, will be generally found to be the result of deterioration of the epithelium. When medicines are given to thicken the blood and excite the activity of certain organs, if their effect is to diminish the quantity of fluids in the body, they generally fail of their purpose; and yet, according to physical laws, the effusion ought to be reabsorbed. In order to bring about this result, the vitality of the epithelium must be modified, by the introduction of irritating substances (as, for instance, in vaginal effusions). On the other hand, the application of physical laws to the functions of the pleura would occasion the formation of a space between its two folds and, consequently, of a constant liquid effusion between them: this effusion takes place only in pathological conditions of the serous membrane, that is, of the epithelium which covers it; for in the normal state this globular layer prevents any passage of fluid and any exhalation from within outwards, exactly as the epithelium of the bladder prevents any passage from without inwards, or absorption.

We may conclude, from all this, that the general property of the epithelial globules is to choose their materials, to borrow certain elements from the surrounding mediums, and reject others. We shall see that the epithelium of the bladder repels fluids generally, without, however, being impermeable in the proper sense of the word; it is impermeable by election, for no doubt, the urine may be concentrated in the bladder, but the water alone is absorbed without passage of the dissolved matter.[1] In the intestinal canal we find that the presence of certain substances, as a solution of sugar or of albumen, produces no effect on the epithelial globule, but that it enters immediately into action if these same substances be modified or accompanied by the gastric juice.

The epitheliums, in short, are essentially *living* elements, as is proved by the metamorphoses and functions found to exist in the whole series of phenomena which we have gone through.

[1] See J. C. Susini, "De l'Imperméabilité de l'Epithélium vésical." Thèse de doctorat, Strasbourg, 1867, No. 30.

B. *The lymphatic system considered as an adjunct to the epithelial functions.*

If the epitheliums are essentially living, they must and do undergo continual changes. Beside the young cells we ought to find old cells, and numerous fragmentary remains of the same; we may be sure that every epithelial globule which exists has been in its place only a short time, and will soon disappear to make room for another; its fundamental character is its ephemeral existence. This fall, this constant change of the epithelial cells is really the means by which some of them fulfil their functions: thus the epitheliums of the glandular *culs-de-sac* are destined to fall continually into deliquium, and thus constitute the phenomenon of secretion.[1]

Apart from the glands, however, the fall of the epitheliums is not a function, but simply a result of their existence. In the epidermis which covers the cutaneous surface, this fall takes place under the form of furfuraceous desquamation, that is, small horny scales (a collection of old, dried-up epidermal cells).

In the mucous membranes desquamation takes the form of a thick ropy fluid product, *mucus*, which has given its name to this large class of membranes. The mucus is less abundant in the normal than in the pathological condition, in which, we might say, the life of the cells is suddenly closed. It is a hyaline elastic substance, resembling the exterior of the eggs of the batrachians, insoluble in water, coagulable by acids, but easily dissolved in alkaline fluids; the application of an alkali to the epithelial membranes has the effect of dissolving the cellular elements under the form of mucus. The chemical composition of the mucus is nearly the same as that of albumen; indeed the albumen of the white of eggs is only mucus of the genital organs of the bird.

The so-called *mucous glands* generally secrete fluids which are very tenuous, and miscible with water, and thus differ greatly from the mucus; the latter is not the product of any special gland, but is the result of the desquamation and fusion of the epithelium; but this shows that we may expect to meet with all the transitions between the mucus properly so called, and the various products of special secretions

[1] See V. Billet, "Généralités sur les sécrétions." Thèse de doctorat, Strasbourg, 1868, No. 129.

(between the buccal mucus and the saliva, for instance). The serosities, found more or less abundantly in the serous cavities, are produced in this way; the *synovia* is the result of fusion of the epithelial articulating membrane; in order to multiply the surfaces on which this fusion takes place, the epithelium of the serous membranes has a great tendency to vegetate, and thus are formed the *epiploic appendages* of the peritoneum and the *synovial fringes* of the articulating cavities. The fluid produced by these surfaces serves to lubricate them; and, as it is observed that the serous cavities show a tendency to disappear when they cease to be the seat of motion, we may infer that their presence is a certain sign of the existence of movements between the surfaces which they line: therefore there must be movements, though they are hardly perceptible, between the dura-mater and the arachnoid, these two membranes being lined by a similar epithelium to that of the serous membranes.

All the waste of the epitheliums cannot, like the epidermal scurf or the mucus, be carried to the exterior, or into the cavities, like the synovia which is, however, partly reabsorbed. Besides, to carry off the waste part of the cells which are placed in the deeper layers, a special apparatus is needed; this is supplied by the *origin of the lymphatic system.* The lymphatic apparatus is composed of a system of vessels, which, if brought together in a diagram similar to that of the blood-vessels, exhibits the form of a cone the summit of which joins the venous system (thoracic duct and great lymphatic vein connecting with the subclavians), while the base (capillaries) is in contact with the epithelium (Fig. 60). The origin of the lymphatic capillaries is still little known; but it is probable that their primitive network is so superficial that the base of the lymphatic cone may be considered as closed by the epithelial membranes;[1] thus, when any substance is placed in the skin, it is, as it were, placed in the origin of the lymphatic system, whence its rapid absorption; in short, it is *inoculated*, and, mixing with the lymph, flows with it into the circulating current. The lymph,

[1] Lately, however, lymphatic spaces have been discovered situated around the smaller capillaries, and hence have been called perivascular spaces. These may be considered as the origin of the lymphatic system. These perivascular spaces, at first having no limiting membrane, gradually coalesce, and form a small lymphatic vessel having a true limiting membrane. [Am. ed.]

or contents of the lymphatic vessels, is a nearly colorless fluid, resembling in appearance the serous fluid of a blister, and holding in suspension a large number of white globules similar to those of the blood.

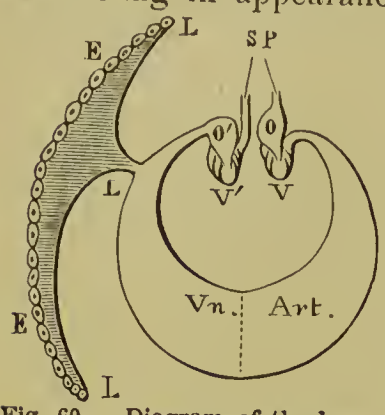


Fig. 60. — Diagram of the lymphatic system.*

The *lymph* which is found in all the lymphatic vessels, and the *chyle*, found only in that part of the lymphatic system belonging especially to the digestive organ (see *digestion*) are not two such different fluids as one might suppose at first sight, and as ancient physiologists considered them (*lacteal vessels* of Aselli and Pecquet; *serous vessels* of Olaüs Rudbeck). Both contain the same elements, and the difference between them is of quantity only, not quality; the difference is, besides, only momentary; after digestion, or at the moment when absorption takes place, the mesenteric lymphatic vessels (chyliferous) contain a larger quantity of the absorbed elements, especially the fats; we must also add that in birds, owing to certain peculiarities in the mechanism of absorption (Cl. Bernard), the difference between the contents of the lymphatic vessels of the mesentery and those of the other parts of the body seems to disappear.

The quantity of lymph contained in the lymphatic vessels (lymphatic cone, Fig. 60), and poured into the blood system, varies greatly, according to the state of repose or activity of the organs from which it proceeds;[1] thus if a lymphatic fistula be made in the neck of an animal, in order to obtain the flow of lymph from the head, we observe that the fluid flows much more abundantly during mastication, than during re-

[1] This is probably due to the fact that by the activity of the muscles the perivascular spaces are alternately contracted and enlarged, setting in motion the lymph towards the larger lymphatic trunks. This current is further facilitated, or prevented from a backward flow, by the valves placed all along the lymphatic vessels. These valves are so arranged that, when thrown out, the fluid passes in a direction from the periphery to the centre. [Am. ed.]

* E, E, E, Epithelial surfaces, base of the lymphatic cone L, L, L; this cone is connected at its summit with the venous cone *Vn.* *Art*, Arterial cone. V, Left Ventricle. V′, Right ventricle. O, Left auricle. O′, Right auricle. S P, Pulmonary system.

pose (Colin).[1] Of course, a still greater difference is observed in the lymph which comes from the intestines, in proportion as the animal is fasting, or in the midst of absorption of the products of digestion.

When the lymph does not contain much fat, it is a fluid slightly opalescent, having a characteristic odor resembling that of the spermatic fluid, and recalling the special odor of the animal to which it belongs; its reaction, like that of the blood, is alkaline.

The morphological elements which it contains, beside the *white globules* and the *globulines*, similar to those of the blood, are the *red globules*, whose presence in certain parts of the lymphatic system can only be explained by transformation of the white lymph globules into red (see page 114); indeed we find all the intermediate forms between these two elements. Finally, we discover, by means of the microscope, numerous particles of fat in suspension animated by the molecular movement called the Brunonian or amœboid movement, and surrounded by a thin layer of albumen (*haptogenous membrane* of Müller), which prevents these fatty particles from fusing with each other and thus forming small drops.

The composition of the fluid part of the lymph appears to resemble closely that of the *liquor* of the blood. It contains fibrine, but fibrine which does not readily coagulate of itself (*Bradyfibrine;* Polli, Virchow), and which is here, as in the blood, the result of a more or less spontaneous separation of Denis's plasmine (Denis of Commercy). — (See page 129). The clot, thus formed, is soft and diffluent: exposure to the air for some time causes it to change its color from white to pink or light red. After the separation of the fibrine a smaller quantity of albumen remains in the lymphatic liquor than in the blood (42 to 1000); but there is, no doubt, some albumen concealed which is not coagulable by heat, especially some forms of *peptones*, which we shall examine when on the subject of digestion; still, the quantity of albumen must be always comparatively small, even in the *chyliferous* ducts; for, according to Cl. Bernard, these vessels absorb very few albuminoids. We reserve the question, however, and shall return to it in studying absorption and the theory of the *peptogens* (of Schiff). In any case, the comparative lack of albumen in the lymph in general appears to indicate that, in

[1] G. Colin, "Traité de Physiologie Comparée des Animaux." 2d edition. Paris, 1872, Vol. II., p. 142.

this respect, the lymph must be considered as formed of that part of the liquor of the blood which is not employed for the nutrition of any of the tissues.

The lymph, in fact, contains excrementitial products of the tissues: it contains extractive matters, especially *urea* (Wurtz), which is found in larger proportion here than in the blood. The urea here appears as the result of the combustion of that quantity which we found was wanting in the liquor of the lymph, in comparison with the liquor of the blood.

The other elements of the lymph are less important: they are salts, resembling those of the serum of the blood (principally chlorides and sulphates). Schmidt even discovered iron, in small quantities, in ashes of the lymph and chyle.

The lymph, like the blood, contains also gases and these are the same as those found in the blood; it seemed at first natural to suppose the proportion of oxygen and carbonic acid in the lymph to be the same as in the venous blood: this, however, is not the case. Recent experiments by Hammarsten have proved that *the lymph contains less carbonic acid than the venous blood.* This fact appears unimportant, but we shall see its significance when treating of the respiratory combustion which goes on in the deeper tissues.

The manner in which we interpret generally the relations of the origin of the lymphatic system to the epitheliums will not apply to all: it applies to the skin, the mucous coat of the mouth, and the mucous membrane in general; but in the small intestine the lymphatic network is separated from the epithelium by a blood network: we shall seek to explain this arrangement later, in reference to absorption. The mucous coat of some organs appears to be entirely without lymphatic plexus: as, for instance, that of the urethra, the bladder, the nasal fossæ, the œsophagus (?) [1] In the deep origins of the lymphatic vessels (connective tissue, muscles,

[1] The existence of lymphatics in the mucous coat of these organs has been the subject of numerous investigations.

According to Sappey, that of the urethra is certainly furnished with lymphatic vessels: they are very fine and thin, and their small branches converge in the frenum of the penis, whence they pass into the ganglions in the fold of the groin; but they communicate behind with the lymphatic vessels of the seminiferous organs and of the testicle, which explains the propagation, even to the scrotum of the *blennorrhagic angeioleucitis* (Sappey). Belajeff carried on his minute researches as to the structure of the lymphatic capil-

bones), we cannot easily admit of its existence, principally because pathological phenomena do not disclose these spaces in the depths of the organs: indeed, the slightest injury to the epitheliums instantly affects the lymphatic system (lymphitis, adenitis); while injury to the deeper organs, the bones, for instance, gives rise to no such complication, unless the disease proceed from the deeper parts towards the surface.

Along the course of the lymphatic vessels are found ganglions, whose complicated structure will be better understood after study of their development: they are originally plexus of lymphatic capillaries, ramified, anastomosed, and rolled up into a ball; the parenchyma, thus formed, retards the flow of the lymph, which crosses it; and the white globules, which are to be poured into the blood, multiply at these points.

The origin of the lymphatic system is another of the subjects on which physiologists are least agreed. The new processes of investigation, however, especially injection of nitrate of silver, have enabled us to solve some points of this important question.

In the first place, it has been demonstrated that, beside the lymphatic vessels subjacent to the tissues, numerous spaces of lymphatic origin are found in the deep-seated tissues, not only in the glands (which are also derived from the epithe-

laries in the lymphatic vessels of the gland and of the canal of the urethra.

The bladder, on the other hand, is entirely without lymphaties. Sappey has shown that the trunks in this organ, described by Cruikshanck and Maseagni, do not begin in it, but in the prostate gland, and, in order to reach the intra-pelvic ganglion, pass along the postero-lateral parts of the bladder. The non-absorption of the vesieal mueus is sometimes explained by this absence of lymphatics, but this is really an essentially epithelial phenomenon.

The lymphatic vessels of the pituitary body have long been a subject of dispute between anatomists. In spite of the descriptions of Cruveilhier, Sappey refused to admit of their existenee, beeause, after injection of the vessels, it was impossible to follow them up to their terminal ganglions. Now, sinee the researehes of Simon, Panas, and Sappey, their existenee ean no longer be denied, for they have been traeed as far as the stylo-pharyngeal ganglions, up to a large ganglion situated elose to the axis, whieh is the highest ganglion in the body (Sappey).

The case is the same with the lymphatic vessels of the œsophagus, but those of the palpebral and ocular conjunetiva are still disputed (Sappey).

lium), but also in the different kinds of connective tissue, which constitute the interstitial tissue of the various organs.

It has been also discovered that in several parts, even in the lymphatics of the surfaces, the connection between the original spaces and the epithelium is not so close as former methods of investigation had led us to suppose: "in all these parts examination of the transparent section of the lymphatic vessels, after injection of nitrate of silver, shows plainly that they are not absolutely situated on the surface of the dermis; as injection of them, and the exaggerated distention caused by the mercury, seemed to show. Teichmann and Belajeff have proved that the entire capillary blood network is always placed above the origin of the lymphatics which, taken together, also form the upper network of the integuments." (Ch. Robin.) Belajeff meanwhile notes that some lymphatic vessels of the urethral mucous membrane advance even to its surface, so as to touch the epithelial polyhedral cells between the papillæ, at their base (!); this appears to be the case, also, in portions of the skin of rabbits, the dermis of which is very thin.

At all events, the perivascular spaces of the lymphatic vessels are closely connected with the capillary system of blood-vessels; in some parts the relation between them is still closer, and the lymphatic and blood capillaries are placed so near each other that, in a section of one of these meshes, we find the lymphatic space surrounding half or two-thirds of the circumference of the blood-vessel: "the lymphatic space has a genuine coat only on one side, being bounded on the others by the blood capillary" (Onimus).

The most signal instance of this arrangement is found in the *perivascular spaces* which Ch. Robin (1858) and His (1863) have described as existing around the vessels of the encephalon. (*Lymphatic sheaths* of Robin and His.) These are tubes, with thin coats and well defined hyaline boundaries, surrounding even the finest capillary vessels, in the white and gray matter of the cerebro-spinal centres, and in the pia mater: this sheath is not, however, found around all these vessels. Their appearance and contents, which consist of a fluid, containing several spherical nuclei (globulines) lead us to believe that these sheaths must belong to the system of lymph spaces, "as they would otherwise form, in addition to the lymphatic, arterial, and venous systems, a fourth vascular system whose terminations and nature would remain

undecided. But, before being absolutely sure that these are lymphatic vessels, we must follow them from their origin, which is known, to the efferent trunks which they form at their junction; and decide the course of these latter, up to their ganglionic termination, as has been done with the other parts of the lymphatic system." (Ch. Robin.)[1] This gap has not yet been filled, and the ancient descriptions of efferent lymphatic vessels of the brain are scarcely demonstrative: Fohmann and Arnold made injections only of the sub-arachnoid cellular tissue; Mascagni appears to have obtained more positive results (by means of the injection of the arteries with the gelatine, and by the transudation of this substance), but he could point out neither the beginning nor end of the vessels which he has described. No one has been able to discover these vessels since; and their existence, therefore, seems very doubtful (Sappey).

The uncertainty of our knowledge becomes still more striking as we approach the question of the structure of the lymphatic capillaries which compose the original network: the most contradictory opinions have been expressed as to the origin of the lymphatic vessels and their close connection with the surrounding tissues, but we can only review them rapidly.

1. The origins of the lymphatic vessels are formed by the *capillary spaces*, previously described, or by prolongations in *cul-de-sac*, similar to the aforesaid capillaries, penetrating the intestinal villosities (*central chyliferi*, or chyle-ducts), the papillæ of the tongue, etc. This view, which was that of Mascagni, Panizza, and Cruveilhier, is now corroborated principally by the researches of Sappey and Robin. The coat of these capillaries is simply a layer of epithelial cells, though some varicosities or other irregularities may be observed; which, in the thickness of certain organs, give them a more or less indented or triangular shape (and might lead to the belief that they are connected by extremely fine links to the neighboring elements); it is only in the large capillaries near the efferent vessels, that we find in addition to the epithelial layer (endothelium) annular fibres, and a hyaline membrane studded with nuclei.

The lymphatic capillaries, like the blood capillaries, thus form everywhere a close network, separated from the other

[1] Robin, article *Lymphatiques;* "Dictionnaire Encyclopédique des Sciences Médicales." 1870.

anatomical elements by an epithelial layer similar to the endothelium of the blood-vessels (Fig. 61): the continuation of this layer shows that their function consists essentially in properties of simple endosmosis or exosmosis; their proximity to the blood-vessels, and the sheath which in many parts they form for these latter capillaries, may show, perhaps, that their use is, not only to bring back to the blood those fluids which are the products of destructive processes, as well as those which have not yet been absorbed by the process of nutrition; but also to become filled with the excess of the plasma of the blood, which enters these capillaries at each systole of the ventricle (E. Onimus).

Many histologists, however, assert that, before the network of the capillaries is formed, or at the level of the most superficial network, the origin of the lymphatic vessels consists of

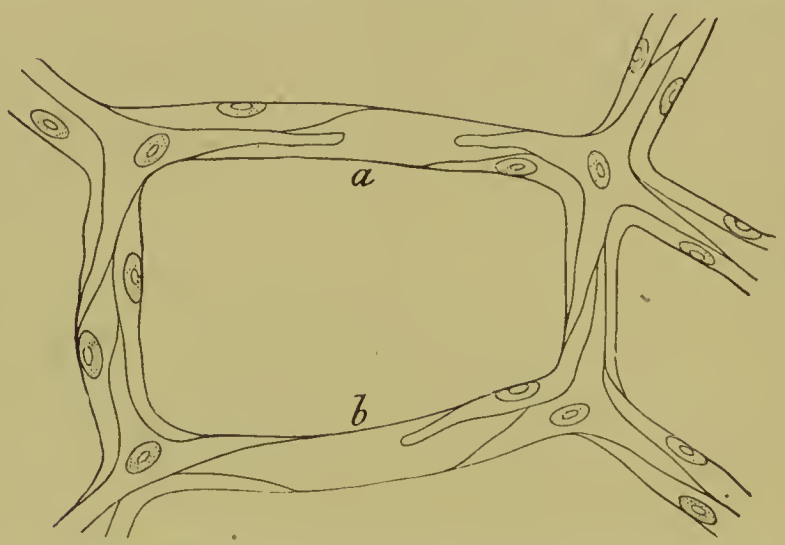


Fig. 61. — Vascular epithelial cells (of the capillaries) impregnated with nitrate of silver.

simple lacunæ partially lined with an epithelium: in this case, the real origin of the lymphatic vessels would consist of the communications between these lacunæ, either with the cells of the connective tissue, or with smaller lacunæ, the network of the interstitial canaliculi of the connective tissue. This view resembles greatly an ancient theory (Hunter, Haase, etc.), according to which hypothesis these vessels took their rise in radicles terminating in absorbing mouths or pores, in the deep tissues as well as on the surface of the serous and mucous membranes; these opinions are now, however, corroborated by experiments and histological re-

searches, which have been nearly all undertaken in Germany, and have produced in some cases "such unlooked-for results that we even feel a sort of hesitation in relating them."[1]

2. *The communication of the lymphatic radicles with the corpuscles of the connective tissue* was first pointed out by Virchow, who found, in a hypertrophied tongue, lacunæ unprovided with genuine walls (lymphatic capillaries), and containing prolongations of plasmatic cells, also hypertrophied. Leydig and Heidenhain have been the principal advocates of this theory; and the latter, in order to explain the absorption which takes place at the point of the intestinal villosities, supposes the existence of a network of plasmatic cells, communicating, on the one hand, with the prolongations of the epithelial cells, and on the other with the central chyle-ducts. Kölliker also embraced this opinion, having tested it by experiments on the lymphatic vessels of the tail of a tadpole, and Recklinghausen's view nearly resembles that of these two writers: according to him the origin of the lymphatic vessels is found in a system of tubes which he calls *plasmatic tubes*, into some of which, situated in the cornea, he made injections, and which he considers as special lacunæ of the connective tissue. Now, according to Kölliker, these lacunæ exactly correspond to those parts specially designated by Virchow under the name of corpuscles of the connective tissue or plasmatic cells; though Recklinghausen persists in considering them as special lacunæ containing cellular elements having no prolongations (and for which he reserves the name of corpuscles of the connective tissue). However this may be, this view tends towards the latest opinion which has been enounced in reference to the origin of the lymphatic vessels.

3. *The communication with the lacunæ of the connective tissue* belongs partly to Recklinghausen's theory, but it has been chiefly upheld by His, Tommsa, and Schweigger-Seidel. According to His, there is direct communication between the capillary vessel and the lacuna, on account of the disappearance of the epithelium of the former: according to Kölliker, the lymphatic capillaries are not *intra-cellular* but *inter-cellular* tubes.

This last opinion is the one which appears destined to tri-

[1] H. Beaunis, "Anatomie Générale et Physiologie du Système Lymphatique." Strasbourg, Thèse d'agrégation, 1863.

umph: it will be found to resemble closely that of Recklinghausen if we carefully distinguish, as he does, what he calls the secretion canals (lacunæ) from the plasmatic cells. In France, this opinion has been adopted by Rouget: he considers the lymphatic vessels at their origin, in full communication with the vacant spaces, the interstices of the tissues. Comparative anatomy shows us, in the inferior animals, circulations which are merely those in lacunæ (sipunculi), and of which, in the superior animals, the only traces are found in the cavernous sinus for blood, and in the lymph spaces for the lymph. On the other hand, the peritoneum must be considered as the remains of what constitutes, in the inferior animals, the general cavity of the body (between the external integument and the internal integument, or the mucous membrane used in digestion): now in the superior animals the lymphatic system still communicates freely, by small openings, with the peritoneal cavity; as was first demonstrated by Recklinghausen. Having placed milk, or some pulverulent substance in suspension in a fluid, on the diaphragmatic surface of the peritoneum, he found that the drops of fat or other granulations passed the epithelial layer at certain points; examination of the peritoneal serous membrane, by the aid of nitrate of silver, convinced him that these points correspond to special *pores*, situated between the cells of the peritoneal epithelium (of the phrenic portion), and leading to lacunæ which form the commencement of the lymphatic vessels of the diaphragm. These facts have been verified in Germany by Ludwig, Schweigger-Seidel, Dybrowshy, Dogiel, etc.; the same experiments were successfully repeated by Rouget, who found that spontaneous injection of colored particles took place in the lymphatic vessels of the diaphragm, when these substances were injected into the peritoneal cavity of the living animal; Ranvier also found that they penetrated these pores, when placed on the abdominal surface of the diaphragm of an animal lately killed.

Recent investigations by Ranvier, however, seem to show that the orifices by means of which this absorption is produced, far from being open when in their natural state, open only at the moment when the reabsorbed particles pass through. The arrangement of these orifices is not plain, as yet: they were supposed to exist in all parts of the peritoneum (Schweigger-Seidel and Dogiel), and even in the mesentery; but, on resuming the subject, Ranvier became convinced that there are neither absorbing mouths nor stomata in these parts, but

really holes, by means of which the two sides of the mesentery are brought into communication with each other. These orifices appear to resemble in structure those which he has described as belonging to similar parts of the epiploön. (For particulars, see Ranvier, "Soc. de Biologie," 1872, and H. Farabeuf, "De l'Epiderme et des Epithéliums," p. 171.)

We may conclude from this that the connective tissue represents one of the principal origins of the lymphatic system, and that the loose cellular tissue may be considered as a vast lymphatic chambered sack, communicating directly with the lymphatic vessels. Pathological anatomy furnishes numerous proofs of this (Ranvier), as well as comparative anatomy, and the study of the development of the lymphatic vessels, and of the tissues called *lymphoid tissues:* thus the boundaries between the *sacks* or *lymphatic reservoirs* of the inferior vertebrated animals and the surrounding connective tissue are scarcely marked, and Meyer considers the former lacunæ of cellular tissue (frogs). As we ascend the scale of the vertebrated animals, and find that the lymphatic system which exists in a distinct form only in these animals, is more and more clearly developed, we see that it arises from modifications of the connective tissue: Leydig found the adventitious tunic of the vessels of the mesentery in many bony fish transformed into areolæ filled with small colorless cells, that is, really, into a genuine lymphatic sheath; the same phenomenon is observed in the adventitious tunic of the arteries of the spleen, the connective tissue of which changes gradually into this lymphoidal reticulum, which constitutes the corpuscles of Malpighi and the lymphatic ganglions.

The structure of the *lymphatic ganglions* is the last proof which we shall mention of the close connection between the lymphatic system and the connective tissue. These ganglions, into the histological study of which we cannot now enter, have been always justly considered as formed by the *clustering of the lymphatic capillaries* (see page 199); close investigation has lately shown that they are essentially composed of connective tissue whose meshes are more or less free, and in which (lymphatic lacunæ) the lymphatic current is diffused, drawing with it the lymph corpuscles (page 198) which are developed in it by proliferation of the plasmic cells, exactly as the globules of pus are developed by similar proliferation in any inflammation of the connective tissue: this explains the resemblance, or rather, the morphological identity, of the pus globules and the lymph or white globules of the blood.

We find besides every transition between the lymphatic ganglions and the connective tissue properly so called: the connective tissue of the intestinal mucous, which is formed of loose trabeculæ, surrounding spaces abounding in white globules, and into which numerous lymphatic capillaries open (*lacunæ*, lymphatic sinus), according to His (*adenoid tissue*), represents the rudimentary tissue of a lymphatic ganglion stretched out and diffused; this tissue becomes compact in places, taking more decided shapes, and forming what are called *closed follicles*, either detached, or joined as in Peyer's patches; their structure has long been recognized as identical with that of the lymphatic ganglions.

The *spleen* is itself a lymphatic ganglion, though of a peculiar kind; it, too, is formed of connective tissue (sheaths of the splenic arteries) changed into adenoid tissue; this tissue, however, is not furrowed by lacunæ or lymphatic sinus; the blood here, is itself diffused through the spaces in the tissue, drawing with it the white globules which are constantly being developed. The particulars of the form assumed by this tissue in order to produce both the Malpighian corpuscles, and the substance of the *pulp* of the spleen, may be found in treatises on histology; but, thanks to the labors of Gray, Billroth, Schweigger-Seidel, and W. Müller, in the midst of all its varieties, the adenoid (lymphoid) connective tissue may always be recognized: it is a collection of lymphatic ganglions or glands, more or less united together, and in which blood-vessels take the place of lymphatic ducts: the spleen is, in short, a *lymphatic sanguineous gland* (H. Frey).

Thus, if the spleen be destroyed or taken away, we observe general hypertrophy of the other lymphatic glands, which appear to prepare themselves to take the place of the spleen, for forming the white globules: this hypertrophy of the lymphatic ganglions has been observed in animals after ablation of the spleen, and in man after it has become degenerate or has been destroyed (Fuhrer).

This rapid anatomical sketch shows us very plainly what are the physiological functions of the spleen; we shall study, later, the indirect and not well understood influence which it exercises on the digestive functions; but in the mean while we must look upon that, as well as all the lymphatic glands, as essentially a centre *of formation for the white globules:* the venous blood of the spleen is also remarkably rich in lymph globules; while the arterial blood which enters it contains

one for every two hundred and twenty red globules, the venous blood which flows out contains one to sixty (His) and even one to five or four. (Vierordt, Funke.) The influence which the spleen exercises in relation to the red globules is still so far from being decided, that some maintain that it is a seat of destruction of these elements (Béclard, Kölliker), while, according to others, it is a laboratory for their production (Funke, J. Bennett).

The following facts are adduced as proofs of its destructive function of the red globules: an animal in which ablation of the spleen has been accomplished, exists longer without food than one which is sound: its blood does not change as quickly into red globules; the lymph which comes from the spleen (for this organ also contains lymphatic vessels) is generally tinged with red. Some observers have remarked a sort of plethora (or hyperglobulia) in animals whose spleen has been removed; but these observations do not agree with the results furnished by clinical surgery.

The red globules are evidently destroyed in the spleen, as in any organ or tissue in which active transformation takes place; this may be readily observed in pathological cases, in which we find a large quantity of remains of the coloring matter of the red globules (*paludal cachexia*): but it is still more likely that a large number of red globules are formed in the spleen, in the physiological condition, in the sense that the white globules which were produced in it, are beginning to change into colored blood corpuscles: indeed, an abundance of globules, in an intermediate state between the white and the red, are found in the splenic veins, as also red globules, possessing all the features which distinguish young elements (small size, less flattened shape, greater resistance to the action of water, etc.).

There are also some glandular organs, resembling, no doubt, nearly the class of lymphatic ganglions and spleen; such as the thyroid gland, the thymus, and, perhaps, the supra-renal capsules; but our anatomical ideas on these subjects are not yet sufficiently precise, and our physiological theories are too hypothetical, to allow us to attempt profitably the study of these so-called vascular blood glands.

PART SIXTH.

DIGESTIVE SYSTEM.

I. Object of Digestion. — Inanition. — Food.

The aim of the digestive functions is to transform the substances borrowed from without, so as to enable them to pass into the system, to be absorbed and carried into the current of the circulation, in order to renew the organs, and keep up their functions.

These reconstructive substances are food.

By privation of food, animals are reduced to a state of *inanition:* the inevitable consequences of prolonged inanition are gradual loss of weight, cold, and death; animals die when they have lost $\frac{4}{10}$ of their original weight (Chossat.)[1]

This loss of weight is produced sooner in some animals than in others: cold-blooded animals will endure privation of food thirty times longer than the warm-blooded, and sometimes, even, for an almost incredible space of time: thus Cl. Bernard has known frogs go entirely without food for nearly three years, while a small bird dies of hunger after two or three days.

Inanition, as observed in persons subjected to a strict diet, not only affects the general temperature, but also the daily variations in temperature: even when there is no fever, this may vary 3°. This fact should be taken into account, in estimating the temperature of persons suffering from intermittent fever, who have long been on a low diet.

Some of the alimentary substances, intended to repair the incessant waste of the system, are immediately absorbed; while others, which are deposited on the surface of the

[1] Chossat, "Recherches Expérimentales sur l'Inanition." Paris, 1843, in 4to.

digestive organs, must first undergo a change, from being subjected to the influence of the juices of these organs. This is because the food, received into the mouth, traverses the different parts of the digestive cánal successively, and is subjected in its course to various mechanical influences, especially that of the different fluids which serve to liquefy and transform it. These modifications are not generally very striking; they appear to affect only the state of cohesion of the substances; insoluble elements being rendered soluble, and coagulable elements incoagulable, etc., while the unchanged parts are thrown off.

No aliment is complete, unless it contains all the elements of which the tissues of the body are composed.

1. Beside their organic principles the animal and vegetable matters which we consume contain various mineral products: such are the alkaline or alkaline-earthy salts, sulphur, phosphorus, iron, all elements necessary to every cell of our organs. Iron is administered to a chlorotic person as food, because iron, which is one of the indispensable elements of the economy, has been diminished in the blood. These mineral substances alone, are incapable of supporting life; and if those which are borrowed from the organic kingdom are found sufficient for this purpose, it is only because they contain in themselves a certain proportion of mineral matters.

The mineral salt that appears most indispensable to nourishment is chloride of sodium. Daily experience proved long ago that man cannot do without this salt, and the religious corporations which sought to subject themselves to the severest privations, tried in vain to banish chloride of sodium from their food. Physiological experiments on animals show (Wundt, Rosenthal, Schultzen) *that this salt is indispensable to the system, and serious consequences have followed its suppression.* Physiological chemistry explains these facts by showing that chloride of sodium enters into the composition of nearly every part of the organism, and is especially indispensable to the constitution of the blood serum and cartilages. It appears to assist in the process of the nutrition of the tissues, and is indispensable to the formation of the bile, pancreatic and gastric juices. Cattle-breeders are well acquainted with the favorable influence produced on the development of animals by administration of chloride of sodium; without asserting that mixture of this salt with the food produces increase of growth and fat, we must admit (Boussingault) that animals fed in this way have more

glossy and thicker hair, a more healthy appearance, are more sprightly and active, etc.

Attempts have been made, but without success, to substitute chloride of potassium for the sodium salt; it has been found, however, instead of possessing the useful properties of the latter, to produce serious injury.[1]

2. The principal aliments are those furnished by the animal kingdom, that is the different forms of albumen, designated under the common name of *proteine substances*, and several other similar elements classed together under the name of *caseines*. All these substances contain Oxygen (O), Hydrogen (H), Carbon (C), and Nitrogen (N), besides a certain quantity of Sulphur (S) and Phosphorus (P), mineral salts, etc. They also contain, probably, iron in small quantities, though this is not yet proved in all cases.

Some vegetable products supply the same aliment, such as *gluten* or *vegetable fibrine*, which is found in many seeds, particularly cereals; *vegetable albumen*, found in emulsive seeds and vegetable juices, and *legumine* or *vegetable caseine*, found in large quantities in the seeds of leguminous plants. These substances may all be classed under the name of *albuminoids*. The transformations undergone by the albuminoid substances contained in plants bear a striking resemblance to those which take place in the animal economy, and which we shall proceed to examine. During the germination of seeds, the albuminoid substances contained in plants give rise to digestive ferments bearing the essential features of some of the ferments furnished by the animal organs. Thus the *diastase* produced by the germination of cereals, closely resembles the fermentation which we shall see takes place in the saliva and in the pancreatic juice.

3. Next come the ternary, non-nitrogenous (or non-azotized) principles containing (C), (H), and (O), in the proportions required for the formation of sugar, starch, dextrine, gum, and various mucilages; all of these substances are incapable of directly forming globules, the prevailing matter of which is nitrogen. These substances are derived chiefly from the animal kingdom; they are also found in animal food, but in very small quantities. Sugar is found in milk, in the liver, and in the blood which flows from this organ; it has been discovered

[1] See Cl. Champy, "Étude comparée de l'Action Physiologique des Sels Potassiques et Sodiques et de leurs Chlorures." Thèse de Strasbourg, 1870, No. 290.

in many epitheliums: in that of the cerebral ventricles are found white granules, some of which, in their behavior with the reagents, resemble amylaceous matter, and others dextrine; sugar also exists in the muscles and accumulates when they are not in action (as after long repose; after section of the motor nerves, and in the muscles of the fœtus), (Rouget). The integument of the non-vertebrated animals is formed of a glycogenous substance: this is the *chitine* of insects, the *tunicine* of the *tunicata* (*animal cellulose*), (Carl Schmidt). These substances are transformed into sugar by boiling with potash (Berthelot, Rouget). All these classes of alimentary substances become capable of being absorbed by contact with the digestive organs.

4. The last class of alimentary substances is the *fats;* these do not require to be *digested*, in the proper sense of the word; that is to say, the digestive juices produce no change in them; *the fats are unchanged.* They may, even, be absorbed by other surfaces than those of the digestive organs, as by the skin, for instance; we know that if fatty substances be rubbed on the skin, they will penetrate the epidermis: this is the only possible mode of nutrition by means of the external integument. The fatty substances are found in both the animal and vegetable kingdom.

Thus we see that nourishment may be derived, almost indifferently, from either the animal or vegetable kingdom: the amylaceous, glycogenous matters, forming almost the essential element of vegetables, are also found in animal products; thus we know that some savage tribes make fermented liquors (alcohol) with the sugar found in mares' milk. We have an instance, on the other hand, of an aliment which is apparently and essentially animal, though found in the vegetable kingdom: in the *cheese* which the Chinese make from legumine (*caseine*) derived from the fruit of leguminous plants.

It is especially important, however, to remark that the property of forming some of these substances does not belong to vegetables only, to the exclusion of animals: the formation of albuminoid substances evidently belongs to both kingdoms; the discovery of animal glycogeny (C. Bernard) proves that animals, as well as vegetables, can and do naturally form amylaceous substances, and the same is true with regard to fatty substances: we owe to experiments by F. Huber, Milne-Edwards, and Dumas, the knowledge of the fact that bees, fed exclusively on sugar, still possess the

property of forming wax, which is a fatty substance. The possibility of an animal organism making any fatty substance used to be denied by many chemists and physiologists.

The animal and vegetable kingdoms also contain substances which resist the action of the digestive juices, and consequently pass through the intestinal canal only to reappear in the excrementitious products, separated from the alimentary principles accompanying them. These are, on the one hand, elastic and connective tissue, the digestion of which is very difficult and even impossible to some persons; and, on the other, numerous vegetable elements the most common form of which is the cellular or ligneous, forming the skeleton of most vegetables, the envelope of certain seeds, etc.

There is, finally, a peculiar class of substances, which must be considered as *aliments*, though they undergo little or no change in passing through the system and the interior of the tissues; they appear to produce the effect of diminishing combustion, or rather of rendering it more efficacious: in short, *they promote the transformation of heat into force*, and render the true alimentary substances previously ingested, more useful. Whence the name of *reserve* or economical aliments, *bearers of force* (dynamophorous). This singular class of substances which are not alimentary, and yet are aids to alimentation, has been the subject of numerous investigations, showing their number and the mode of action peculiar to each. *Alcohol* stands at the head of this class: according to many physiologists alcohol is burned in the system, serving thus to produce heat immediately (Liebig, Hepp, Hirtz, Schulinus); but recent investigations of Lallemand and Perrin show that if alcohol be received into the system it merely passes through it, and is always found again, as in the blood and tissues, especially the nervous tissue, in which it appears to take up its abode for some time: in short, it is not consumed, and its presence as an alimentary substitute only serves, by economizing combustion, to increase its utility. We can understand thus, that alcoholic drinks may be indispensable, in some degree, to a man who is obliged to perform severe labor, with insufficient nourishment; as to the fatal excess which so often succeeds a moderate use of these drinks, physiology shows us that our efforts should be directed less against this, than against the conditions which make the use of alcohol an imperious and fatal necessity for the working-man (Moleschott).

After alcohol come the active principles of tea, coffee, and similar drinks: theine, cafeine, theobromine, coumarine (tonka bean), the principle of Peruvian *coca*.[1] This latter substance appears to affect the muscular system especially, while the former have more influence on the nervous system. Messengers, travellers, and workmen have found that by chewing the leaves of the *erythroxylum coca* they could dispense with any solid or liquid food for one or two days: these leaves allay hunger and thirst, and sustain the strength. This is the reason that the Peruvians deified this tree, leaves of which were afterwards employed by the Incas for money. Ch. Gazeau,[2] however, maintains that this so-called power of fasting is only anæsthesia of the stomach and œsophagus, and that the person is *autophagus*, and in a state of inanition without being aware of it. But as hunger is a universal sensation of the system, it is scarcely possible to maintain this theory, in the face of the well-known instances of nutrition being kept up by cocoa as well as by alcohol. The action of these latter substances cannot be explained by referring it to the presence of nitrogen in their composition and regarding them as azotizing aliments, the plastic aliments of Liebig. Cafeine, theine, etc., contain a large quantity of nitrogen, but their composition closely resembles that of the uric acid, xanthine and hypoxanthine, all of which are excrementitious products or waste from the organism: it thus appears that theine, cafeine, etc., merely pass through the organism, and reappear in the excreta, and this has been proved by experiment.

Liebig's *extract of meat* must also be classed among the economical aliments (*aliments d'épargne*), if, indeed, this product can be said to have any alimentary utility at all. This extract is now shown to be in no way nutritive. The nitrogenous crystallizable principles which it contains are no more nutritive than theine or cafeine, etc.; the only use of this extract is that of a slight stimulant from the salts which it contains (nearly one-fifth of its weight). In short, Hepp and Müller's experiments (Thèse de Paris, 1871) on animals, seem not only to show the uselessness of this extract as an article of food, but also to ascribe to it a poisonous effect, when taken in large

[1] Ch. Marvaud, "Etude de Physiologie Thérapeutique, Effets Physiologiques, et Thérapeutiques des Aliments d'Epargne ou Antidéperditeurs. Alcool, Café, Thé, Coca, etc." Paris, 1871.

[2] Ch. Gazeau, "Nouvelles Recherches Expérimentales sur la Pharmacologie, la Physiologie, et la Thérapeutique de la Coca." Thèse de doctorat, Paris, 1870.

quantities: according to Kemmerich the exclusive use of the extract of meat would kill sooner than starvation.

In studying the different phases of the act of digestion, we will take, first, those which are observed in the sub-diaphragmatic part of the canal; next, those of the cavity of the stomach; and, finally, phenomena which take place in the passage through the intestinal tube (large and small intestine).

II. First Part of the Act of Digestion.

The aliments introduced into the cavity of the mouth are divided by the teeth (*mastication*), moistened and modified by the saliva (*salivation*), and then carried into the pharynx, seized by it, and pushed into the stomach by the œsophagus (*deglutition*).

A. *Mastication.*

The purpose of mastication is to divide the solid aliments so that they may be more easily attacked by the digestive fluids of the mouth and other parts of the intestinal canal. Meat and nitrogenous substances are more easily digested in the stomach after they have undergone mastication in the mouth, but the operation need not be carried very far in the case of aliments of this kind: thus we observe that the exclusively carnivorous animals have no teeth properly so called, but merely hooks, with which they tear their food into large pieces. Mastication is indispensable, on the contrary, in the case of aliments belonging to the vegetable kingdom; the greater number of nutritive vegetable matters are enclosed in a casing which generally resists the action of the digestive juices: the masticating system serves to tear the cells, the envelope of seeds, etc.; *prima digestio fit in ore*, said the ancients: in saying this, they spoke only of mastication, being ignorant of the chemical process which takes place during salivation.

The *lower jaw*, as it rises and falls, represents a *lever*, moving round a supposed axis, which, in movements of slight extent, is centred in the condyles; but when the mouth is wide open, the separation of the jaws is greater, and the condyles quit the glenoid cavities, and come further forward. The movement then takes place round an axis crossing the two upright branches of the inferior maxillary at the level of the dental *foramen*; however little the buccal cavity may be opened, and even in ordinary mastication, the two

movements are combined, as may be proved by placing the finger on the temporo-maxillary articulation : the rotation of the condyle in the cavity, and its forward projection take place at the same time; so that it is difficult and even impossible to decide exactly on a fixed axis around which all the movements of the jaw are made.

In all cases the *lower jaw* acts as a *lever* of which the fixed point is behind, in the upright branch of the bone; the point of application of the power, which is represented principally by the *masseter* and *temporal* muscles, is in the front edge of this upright branch; the resistance may be found in different points: if an aliment is to be divided, the resistance lies on the level of the incisors, and in this case the lever belongs to the third kind, and the arm of the power is very short in comparison with the arm of resistance (see p. 103, mechanism of the muscles). When the food requires to be ground, the resistance is applied at the level of the molars, and its lever arm becomes shorter, thus giving the advantage to the action of the power, the lever arm of which keeps its original length. Even in the case of a resistance opposed to these latter molars, the fibres of the masseter may be found anterior to the resistance; and the maxillary lever then becomes a lever of the second kind, that which is most favorable to the action of the power (*interresisting lever*, page 102).

There is also a *side movement* in the lower jaw, which is restricted in man, but of great extent in the ruminants. It is due to the contraction of the external pterygoid muscle which, by drawing one of the condyles forward, brings it out of the glenoid cavity, while the jaw pivots on the other condyle.

We see thus, that in man mastication is a compound action, resembling both that of the carnivora and the herbivora (ruminants), on accounnt of the compound nature of his food: the carnivora, which only tear their prey, make no upward and downward or sideway movement; thus their condyle turns only on its transverse axis. In the ruminants the sideway movements are very decided, and for this purpose the condyle is flat and movable in all directions. Another type of condyle is that of the *rodents*, the antero-posterior diameter of which is of great extent, a glenoid cavity being hollowed out in the same direction. In man, the form of the condyle is intermediate between all these, while the masticatory movements are more varied, and

are combined in a more complex manner than in any other animal.

Beside the action of the jaws in tearing, cutting, and crushing the food, there is also an action of the *tongue*, *lips*, and *cheeks*, which aid mastication by pushing the food between the teeth, and keeping it in place.

Mastication is a voluntary act, and yet it may be said to belong, in some respects, to the class of reflex actions: thus mastication becomes slow, difficult, and even impossible, when there is an insufficiency of saliva, or when the want of food is not felt. There must, then, be here as everywhere, a special peripheral impression, which, being reflected in the nervous centres (the bulb, in mastication), causes the phenomenon of reflex action. Mastication, like walking and many other movements which are, apparently, quite voluntary, is performed, in a great measure, and during most of the time, by means of the mechanism of reflex actions. (See page 45, *Physiology of the nervous centres: bulb.*)

B. *Salivation.*

The organs of salivation are not only the salivary glands properly so called, but the whole glandular system spread throughout the cavity of the mouth: such as the molar glands, or glands of the cheeks, the glands of the lips, those of the under surface of the tongue, those of the roof of the mouth, and those of the velum of the palate, which are improperly called mucous glands. All these glands are formed by masses of globules arranged in ramified tubes, opening, sometimes, singly to the outside, and, at others, uniting in a single excretory tube, *Steno's duct* (parotid), *Wharton's duct* (sub-maxillary). The saliva is a deliquium, produced by the fusion of the globules of these glands as they fall into decay.

The salivary juice is found to differ slightly in the different glands, but it has one general feature, that of being very watery, and, in this respect, differs greatly from the mucus; it is water, containing scarcely from one to two per cent of solid matter; its reaction is *alkaline:* when taken from a person in a fasting condition, it is sometimes found to be slightly acid, but this acidity is simply owing to decomposition of the food remaining between the teeth.

The saliva contains an organic nitrogenized (azotic) substance (discovered by Leuchs, 1831); it is not well-defined, but is a peculiar form of albuminous substance called *ptya-*

line (Berzelius) or *animal diastase* (Mialhe), resembling closely the principle of sprouting barley. This substance has the property of changing *starch* into glucose. The parotid saliva alone has no power to change starch into sugar (in the horse, and in man); the case is the same with the sub-maxillary gland (the dog): the power of turning substances into sugar thus appears to belong to the *complex product* of the different salivary glands and of those glands, called mucous, which are so abundant in the buccal cavity. This property does not appear to belong exclusively to the saliva: it is found in nearly all animal substances; the mucous of the bladder, the blood, and the muscular flesh all have it though in a low degree.

The saccharizing property of the saliva is not equally prominent in all animals: man is one of the most favored in this respect, but less so than some of the herbivora, especially the guinea-pig; the saliva of the dog, so often made use of for experiments, is not well adapted for this purpose, possessing the property, as it does, in a much lower degree than many others. In man, this property is developed only with the first appearance of the teeth (Bidder). The ptyaline of the saliva can only be extracted by precipitating it by alcohol, and then redissolving it in water (general process of separation of the albuminoid ferments). In all salivary ptyaline are found peculiar elements of a globular form, called by some authors *pyoid globules*, and closely resembling the white globules. Leeuwenhoek had already discovered these globular elements, which exhibit decided phenomena of amœboid movements, and are reproduced by means of fission; these inferior organisms may be compared to ferments, and have a more or less direct part in producing the chemical activity of the saliva; indeed we notice that the more abundant these organisms are, the greater is the saccharizing property of the saliva; thus, in salivation (ptyalism) produced by the use of mercury, Leeuwenhoek's corpuscles are extremely numerous, and the saliva has the property of changing starch into sugar in the highest degree (Rouget).

Ptyaline is a soluble ferment; it partakes of the nature of an albuminoid, but differs a little from other albuminoids in not being precipitated by a heat of 60° (C); this does not, however, imply that it is not destroyed by an increase of temperature (Frerichs, Cohnheim), but the temperature must be raised at least to the boiling point in order to effect

this (Schiff); Cohnheim has attempted in vain to prove that ptyaline is not an albuminoid substance.[1]

The other elements of the saliva are salts, identical with those of the blood, and also *sulphocyanide of potassium.* The existence of this salt, first discovered by Treviranus, has since been the subject of much dispute: the reaction by which it is distinguished (red color produced by salts of iron) has been attributed to acetates; but distillation of the saliva proves that it contains no acetic acid. It was then supposed that the sulphocyanide was the result of decomposition or was produced only in pathological cases (hydrophobia in dogs) or under the influence of certain nervous or moral conditions (Eberle). But closer investigation of the subject by Longet, Œhl, Sertoli, and Schiff has shown that sulphocyanide is an element which is always present in human saliva, though its use is not yet understood.

The secretion of the saliva offers a good example of the influence exercised by the innervation of the secretions. This secretion indeed is not the result of irritation directly produced by the food; the large salivary glands are too remote from the buccal mucous. A reflex phenomenon takes place here. The peripheral impression produced by the food is transmitted by a special nervous organ to a reflecting centre, whence it is communicated to another organ (centrifugal nerve) which determines the secretion. This reflecting centre is not, as was long supposed, situated in the ganglions of the great sympathetic nerve: numerous experiments have proved that it is in the spinal cord.[2] The centripetal nerves beginning in the mucous membrane, go to the bulb: these are essentially the branches of the trigeminus. This function is best shown by experiments on the nerve fibre called the *lingual*, which is a branch of the inferior maxillary; but the glosso-pharyngeal and pneumo-gastric nerves also take part in the centripetal conduction; for excitations of the stomach cause secretion of the saliva, and we know that vomiting is

[1] See E. Ritter, "Des Phénomènes Chimiques de la Digestion." Thèse de Concours, Strasbourg, 1866.

[2] Cl. Bernard believed that he had proved that the sub-maxillary ganglion may serve as a centre of salivary secretion, and this was generally considered a sufficient reason for asserting that the ganglions of the great sympathetic nerve possess the property of *reflex centres;* but this opinion can no longer be held in the presence of Schiff's contradictory experiments. (See Schiff, "Leçons sur la Physiologie de la Digestion." Florence, 1866.)

always preceded by an increase of saliva. If a section of the lingual be made, we find that irritation of the peripheral part of the nerve which has been cut produces no effect on the formation of the saliva, while excitation of the central extremity, which is still connected with the spinal cord, is certain to excite the secretion. The nerves which extend from the bulb to the salivary glands, are fibres of the facial nerve, especially the *chorda tympani:* this latter nerve belongs particularly to the sub-maxillary gland.

Excitation of the great sympathetic nerve may also cause secretion of the saliva, but this does not appear to take place normally, under reflex influence. The saliva produced in experiments, by the action of the great sympathetic nerve, is much thicker than the normal saliva. This fact must be compared with what takes place at the same time in the vessels: when the great sympathetic nerve is excited the vessels of the gland become constricted (contracted), while the contact and exchange between the blood and the secretory elements appear more intimate, since the blood which flows from the gland is found to be quite black. On the other hand, when the sub-maxillary gland secretes its fluid products, under the influence of the facial nerve (chorda tympani), we find the blood-vessels greatly dilated (paralyzed) and the blood which flows from them red, almost as in the arterial system (Cl. Bernard).

Too much importance must not, however, be ascribed to the presence of the blood and the state of the vessels; we have already shown that the secretion of the saliva is an instance of the immense attraction exercised by the secretory globule over the surrounding substances. If the circulation be suppressed, we may, by irritating the centripetal or centrifugal nerves of the glands, cause the production of a considerable quantity of saliva (Ludwig). The globule then imbibes the materials for its support from the tissues which surround it: it possesses great power of attraction, by which it gives rise to the currents flowing towards it, across the inert membrane which forms the coat of the secretory tubes.

Thus the state of arterial pressure is only secondary. The saliva is the result of a deliquium of the cellular elements of the glandular epithelium, and in this case we must consider the gland simply as a filter.[1] This deliquium is pro-

[1] V. Billet, "Généralités sur les Sécrétions." Thèse de Strasbourg, 1868, No. 129.

duced by the action of the nervous system, and nervous terminal ramifications have lately been discovered, penetrating the glandular epithelial element (Pflüger).

Many physiologists maintain that the nerves affect the secretion of the saliva only by their function as vaso-motors. The question of the vaso-motor nerves that cause dilatation of the vessels (see p. 173) here again presents itself. The belief is, however, constantly growing into favor, that the influence of the nervous system on secretion bears directly on the globular elements of the secretory pouches or bags (*culs de sac*), but we must add that Pflüger's researches on the subject of the termination of the nerves in the glands are by no means calculated to produce conviction: this histologist supposes that the nerve branches terminate in the so-called glandular *culs-de-sac, preserving even here their central nerve substance* (myeline); were this the case, it would be an exception to the general rule, for, when a nervous filament approaches its real termination, it usually lays aside its myeline, retaining only its axis-cylinder, and sheath of Schwann. This fact leads us to suppose that Pflüger did not discover the real terminations of the secretory nerves.

On the other hand, histologists have made great efforts to observe the act of fusion of the globular elements of secretion at the moment when this takes place, or at least to ascertain what changes appear in the epithelium of the glands after abundant secretion: Boll, Giannuzzi, and more particularly Heidenhain and Ranvier, devoted themselves to the study of this subject. Giannuzzi discovered in the salivary cells peculiar prolongations in the form of pedicles, which are bent round in a curve, and joined on to the enveloping membrane: he found also, in the glandular *culs-de-sac*, between the enveloping membrane and the salivary cells, properly so called, these peculiar formations he calls *half-moons* (or *crescents*) being special cells, flattened in shape, and with one or two nuclei (in course of proliferation). The purpose of these elements is not known. Heidenhain has observed that we find in a gland, after abundant secretion, in place of the large salivary cells, some which are much smaller and quite granular; he supposes that the larger cells are destroyed in order to form the substance to be secreted, that the remains escape with the salivary fluid, that the small new elements arise from Giannuzzi's crescents, and that these are intended to take the place of the salivary globules which have been destroyed. Ranvier states that after abundant secre-

tion the glandular *culs-de-sac* decrease somewhat in size, and that the mucous (salivary) cells *empty their contents gradually without being destroyed.* "In short," he says, "the product secreted by the glands arises from their cells, in order to form which the glandular cells simply yield up the substance which has been elaborated within them, and are not entirely destroyed, as Heidenhain has affirmed. Their active part (nucleus and protoplasm) still remains, and it is this, probably, which makes up for the waste occasioned by secretion.[1]

Some agents may cause secretion of the saliva by exciting metamorphoses of the epithelium of the gland, as they excite those of the epithelium of the mouth in general: it is in this way that *mercurial salivation* is produced.

The excretory tubes of the salivary glands appear to be deficient in muscular elements: the saliva flows, not by a movement similar to the peristaltic movement, but by a sort of *vis a tergo* of the fluid, which, first filling the lower part of the salivary tubes, rises gradually, and at length overflows.

The nerve centre of the salivary secretion is found, as we have said, in the spinal cord; under certain circumstances the intervention of other nerve centres must be admitted: the encephalon, as the organ of the imagination, has great effect on the secretion, and the sight or mere remembrance of food will suffice to increase the effect. Still, properly speaking, the will has no power to produce this secretion: the imagination must call up the memory of a gustatory impression, or produce movements in the mouth which are capable of producing secretion by means of reflex mechanism. Under different circumstances, the encephalon appears, on the contrary, to act against secretion by paralyzing the excitatory nerves. Thus, certain emotions of the mind will hinder the secretion of the saliva, while others increase it. Strong emotions produce this effect; which is shown by excessive dryness of the mouth, and, sometimes, almost entire inability to speak.

The secretion of the saliva is also more or less under the mechanical influence of the neighboring organs: thus the movements of the jaw, and contraction of the muscles of the

[1] Ranvier, "Notes à la Traduction Française de l'Histologie de Frey," p. 439.

velum of the palate, by acting on the corresponding glands, cause secretion of the saliva.

Beside the chemical effects resulting from the presence of the animal or ptyaline diastase, the principal use of the saliva is found in the mechanical part which it takes in mastication, the solution of sapid substances, the lubrication of the passages which the food must traverse and of the food itself. We shall presently see that the saliva is essential to deglutition; for this purpose, it must accompany even those aliments which are not chewed, and upon which it produces no chemical effect. This explains the presence of the salivary glands in the carnivorous animals, in which the saliva is not called upon to act on aliments which are essentially nitrogenous.

Cl. Bernard, perhaps a little exaggerating the mechanical property of the salivary fluid, at the expense of its chemical function, assigns to each saliva a peculiar, corresponding, mechanical function, associating each of them with one of the three physiological phenomena of mastication, deglutition, and gustation.

The parotid is the masticatory gland: it exists only in animals which have teeth to grind their food; it is found to be larger as trituration is slower and more difficult; finally, the parotid secretion takes place especially during the movements of mastication; and when the animal chews, first on one side and then on the other, the parotid situated on the masticating side always secretes most abundantly (Colin).[1]

The sub-maxillary secretion belongs only to the phenomenon of gustation: the most certain method of producing this secretion in experiments is to place a sapid substance on the tongue, and thus to excite the reflex action which we have described above; in comparative anatomy we find that the sub-maxillary gland disappears wherever there is no need of gustation: it is largely developed in the carnivorous animals, while it disappears almost entirely in the granivorous birds.

Finally, the sub-lingual gland, the secreted product of which is thick, ropy, and similar to that of the different buccal glands, called mucous, in the same way is more particularly connected with deglutition: it serves to unite the

[1] Colin, "Traité de Physiologie comparée des Animaux." 2d edition. Paris, 1871, Vol. I. p. 601.

elements of the food received, and to lubricate their passage along the tongue, and the isthmus of the fauces.

These distinctions, which appear so ingenious and natural at first sight, Schiff has shown to be, perhaps, a little too sharply defined; thus, mastication alone, — that is, not accompanied by any gustatory impression, — has little or no influence on the parotid secretion: in the case of all the salivary glands, the impression of taste, joined to the masticatory movements, are the most powerful means of producing secretion.

The *quantity* of saliva secreted in a day has been variously estimated on account of the intermittent form of secretion. In dogs, it is as much as 1500 grammes. This secretion though more especially sensible during mastication, however, is continuous; because the saliva is necessary to keep the mouth moist, to assist the movements of the tongue (speech), and, as we have already said, for the purpose of deglutition. We shall find that, by means of the saliva, movements of deglutition are produced from time to time and at very short intervals, the purpose of which is to preserve the function of the organ of hearing.

C. *Deglutition.*

When the food has been so mixed with the saliva as to become capable of movements like a fluid, it is subjected to a pressure, which forces it downwards, from the buccal cavity to the cardiac orifice of the stomach; in other words, it leaves the mouth, and passes through the pharyngeal and œsophageal tubes. The principle governing the movement of the food is the same as that which governs the movement of fluids, that is, excessive pressure at one point and none at all at others, thus destroying the equilibrium of the fluid, and causing it to flow in the direction in which the pressure is slightest. This principle applies to the deglutition of solids, the state of semi-liquefaction into which they are brought imparting to them mechanical properties similar to those of fluids.

The organs of deglutition consist (Fig. 62), first of the buccal cavity, — bounded, above, by the roof of the mouth; at the back, by the velum of the palate; below, by the tongue; and, in front, by the teeth. After the buccal cavity, we come to the pharynx, at the level of which the alimentary canal communicates with the windpipe; or, rather the two passages cross each other (communication from above and behind with the nasal chambers — the first part of the windpipe;

below, and in front, with the larynx — the continuation of the wind-pipe). A most important feature in deglutition is the

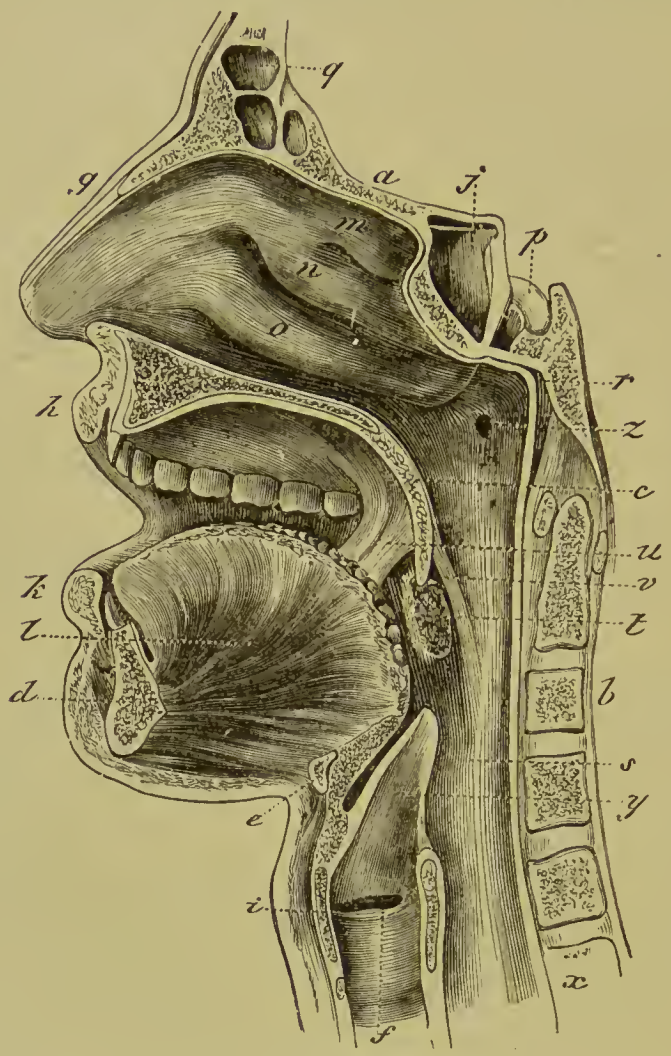


Fig. 62. — Mouth and pharynx.*

mechanism by which the upper and the lower orifices of communication become obliterated.

When mastication and insalivation are completed, the food collects in a single mass on the surface of the tongue, the tip of which touches the roof of the mouth while the

* *k*, *h*, Buccal aperture. *l*, Tongue. *d*, Lower jaw, with the genio-glossal inserted. *e*, Hyoid bone. *y*, Epiglottis. *f*, Cavity of the larynx (with the opening of the ventricles). *c*, Velum palati. *u*, Anterior pillar of the uvula. *v*, Posterior pillar. *t*, Tonsil. *s*, Narrow part of the pharynx, connected with the œsophagus. *z*, Orifice of the Eustachian tube, at the upper part of the pharynx.

food passes downwards to its base. As the food reaches the front pillars of the velum of the palate — being pushed into the pharynx by the tongue laid against the roof of the mouth — it is seized by the pharynx, which rises before it, on account of the contraction of its longitudinal fibres. The circular fibres of this muscular tube immediately contract successively, and drive the food before them into the œsophagus, where it continues its progress by means of a similar peristaltism — that is, successive contraction of the circular muscular fibres, driving the food before them, while the contraction of the longitudinal fibres draws towards it those parts of the tube in which it is to become involved.

While the food crosses the pharynx, the two communications between this tube and the windpipe are obliterated.

The upper communication (pharynx and nasal chambers) is not obliterated by a movement of the velum of the palate resembling that of a drawbridge, as was for a long time supposed (Bichat); it takes place by means of the *posterior pillars* of the velum of the palate. In order to effect this obliteration, the pillars approach each other: while the muscular fibres of these pillars (pharyngeal muscles) are directed

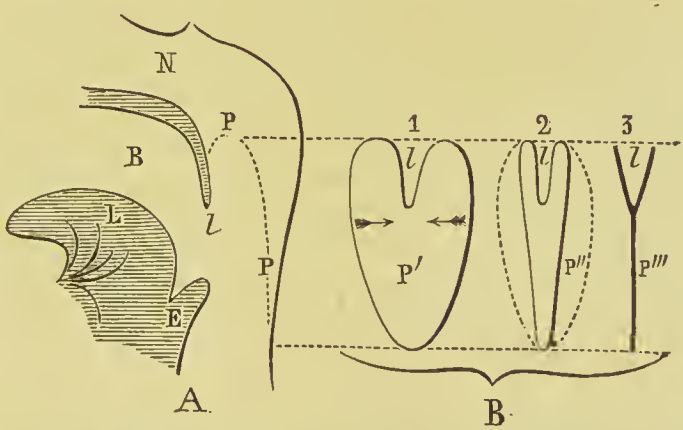


Fig. 63. — Diagram, showing the occlusion of the naso-pharyngeal passage, by the action of the muscles of the posterior columns (*Staphylo-pharyngeals.*)*

obliquely, downwards and backwards, across the lateral walls of the pharynx, and are again joined together, along a considerable part of the posterior median line, so as to form an

* A, This part is seen in profile. N, Nasal cavity. B, Mouth. L, Tongue. E, Epiglottis. *l*, Uvula. P, P, Course of the staphylo-pharyngeal muscle.
B, Diagram of the orifice, enclosed by the two staphylo-pharyngeals as by a sphincter. 1 (P′), In the state of repose. 2 (P″), Semi-occlusion. 3 (P‴), Perfect occlusion. *l*, Uvula.

elliptic sphincter, in an oblique line from front to back and from top to bottom. (Fig. 63.) The anterior and posterior extremities of this elliptic sphincter being nearly fixed, its orifice can only be obliterated by reducing it to an antero-posterior slit. By means of this movement the two sides of the velum of the palate resemble two curtains drawn together, the pharyngeal muscles, which are concave when in the state of repose, having their curve reduced to a straight line; and representing in this state of contraction the string of the bow which they represented when in the state of repose (Fig. 63; B, 2); an opening still remains, however, more or less wide, but this is obliterated by the contractions of the middle and inferior sphincters of the pharynx. The uvula, finally, is intended to close any crack which may still remain open, but it is not indispensable (Fig. 63, B, 3, *l*). By means of these movements, some idea of which was formed by Albinus and Sandifort, though they have been most clearly demonstrated by Gerdy and Dzondi, the occlusion of the isthmus of the fauces is made even hermetical. Indeed, if the nostrils be stopped up during deglutition, we find that hearing is slightly obstructed. This is because, during the succession of peristaltic movements of the pharynx, its upper part is inclined; and, as the pharyngeal sphincter still remains shut, rarefaction of the air in the nasal chambers ensues.[1] But as, during deglutition, the base of the velum of the palate is stretched out and fixed by the contraction of its superior muscles, and thus opens the Eustachian tube, it follows that the rarefaction of the air of the nasal chambers is communicated to the tympanic drum, and kept up until a fresh movement of deglutition places this drum in communication with the freely opened nasal

[1] This fact of the rarefaction of the air suggested to Maissiat (1838) a singular theory of deglutition, which has been refuted by the explanation given here. Maissiat maintained that when deglutition takes place a vacuum is formed in the cavity of the pharynx by means of its rising and subsequent enlargement: the food is precipitated into this cavity by the pressure of the atmosphere, forming what Maissiat calls the *involuntary jerk* (*saccade*) of deglutition.

This phenomenon does occur; but, in the first place, it is not in the pharynx, properly so called, but in the naso-pharyngeal cavity; and, in the second, the formation of this vacuum does not correspond with the rising of the pharynx, but with its descent; not at the beginning, but at the end, of deglutition.

chambers. This shows how complete is the obliteration of the isthmus of the fauces; and it may also be shown by means of a tube communicating at one end with the nasal chambers (the nostrils being closely pressed against the tube), while the other end is immersed in water (experiment by Maissiat): at each movement of deglutition the water rises in the tube, on account of the rarefaction of the air of the nasal chambers (by the descent of the constricted isthmus of the fauces); this rarefaction is communicated to the air in the tube, as it is to that in the hollow of the tympanum.

The isthmus of the fauces thus undergoes a triple change during deglutition: it closes by the contraction of its constrictors; it rises slightly as deglutition begins; and descends slightly as this is finished. This rising and falling is produced by the simultaneous movement of the pharynx. The descent explains the vacuum produced in the closed nasal chambers: the ascent shows us why a probe introduced horizontally into the nasal chambers, as far back as possible, will be slightly pushed forward as each movement of deglutition begins (experiment by Debrou); this led Bichat to believe that there was some disarrangement at the top of the velum of the palate, and others that the velum is simply raised; but we have seen that not only the velum, but the whole isthmus of the fauces when constricted, rises and sinks again immediately.

The occlusion of the antero-inferior orifice of communication, or orifice of the larynx, is effected by means of the *epiglottis*, which, when free, leaves the respiratory orifice uncovered, but, as it is formed of elastic tissue, bends under the weight of the food as it passes. The epiglottis is not, however, indispensable to this obliteration. As the pharynx rises, the larynx, sharing the movement, strikes against the base of the tongue (which is there protuberant), and this mechanism is sufficient to protect the respiratory orifice, or at least to secure the retroversion of the epiglottis over it. The small cartilages placed above the arytenoid cartilages join with the epiglottis in effecting the occlusion of the opening of the larynx.

The absence of the epiglottis is scarcely any hinderance to the deglutition of solids: the movements of the whole larynx under the cushion, at the base of the tongue, suffice to protect the respiratory orifice. The case is not the same, however, with the deglutition of fluids, and this shows us the purpose of the epiglottis. When the deglutition of a mass

of fluid is completed, the larynx resumes its natural position; but some drops of the fluid always remain on the back of the tongue, and, uniting together, flow into the œsophagus; these would inevitably fall into the larynx but for its membranous lid (the epiglottis). Clinical observations and the results of experiments, however, often appear contradictory on this point; since we find that sometimes a fit of coughing, and at others, no disturbance at all, will follow the deglutition of a fluid in invalids or animals who have been deprived of their epiglottis (Magendie, Longet). The varying nature of these results is easily explained. In man, the epiglottis may be destroyed by so many different causes (wounds, syphilitic erosions) that no two cases can be compared, and one person will suffer no inconvenience, while in another alarming symptoms will follow the deglutition of a fluid. The different results produced in animals by the deglutition of fluids, after the epiglottis has been carefully removed, is explained by the fact that, whenever the animal is calm after deglutition, no disturbance follows, while serious consequences ensue if it is agitated in any way. Schiff has demonstrated that, when the deglutition of fluids is apparently finished, the accumulation of drops remaining on the tongue, which descends to the glosso-epiglottal ligaments, gives rise to a second series of movements of deglutition, repeated two or three times, until not a drop of the fluid remains. Now, if an animal be disturbed while drinking, in however slight a degree (as, for instance a dog may be prevented from licking himself, after swallowing a bowlful of milk) this secondary deglutition does not take place, and if the epiglottis have been removed, the drops of fluid remaining on the tongue, may be introduced into the larynx, and occasion coughing. In short, entire excision of the epiglottis in the dog, does not interfere with the deglutition of fluids, if only that subsequent deglutition takes place, which serves to rid the isthmus of the fauces of those fluid particles which still adhere to it.

Though solid or liquid particles of food sometimes find their way into the larynx, it rarely happens that they penetrate into the trachea: as soon as they come into contact with the mucous membrane of the vestibule of the larynx, the peculiar sensibility which the superior laryngeal nerve imparts to this region is excited, giving rise to the phenomenon of coughing, by means of which these particles are instantly expelled. The exquisite sensibility of the vestibule

of the larynx thus has an important share in the protection of the respiratory organs (Longet); it is intended to prevent the entrance of foreign bodies into these organs, an occurrence which the animal would have no power to prevent, if the opening of the glottis were once passed (see larynx and obtuse sensibility of the trachea).

A final obstacle to the entrance of these bodies into the trachea is found in the fact that the opening of the glottis closes whenever deglutition takes place; this occlusion is, however, only a precautionary measure; and it must not be supposed that, in the normal state, the substances which are being swallowed come in contact with the edges of the glottis. Magendie, who first discovered this closure of the glottis during deglutition, attached too much importance to it, and was mistaken as to the mechanism by which it is produced, attributing it to the muscles of the larynx, in this special case (arytenoid, aryteno-epiglottidean) innervated by the upper laryngeal nerve. Longet, who understood the subject, has shown both the accessory importance of this occlusion and its mechanism, which consists in the movement of the thyroid cartilage by means of the contraction of the sphincter muscles of the pharynx. *The movements of the glottis accompanying deglutition are thus subjected to other muscular agents than those which act upon this same orifice, during the production of the vocal and respiratory phenomena.* (Longet). Finally, Claude Bernard has completed the study of this interesting question, which here we can only sum up rapidly, by showing that the spinal accessory nerve innervates the inferior constrictor muscle of the pharynx in order to produce this occlusion of the glottis; and we can thus add to Longet's conclusion, that the nerves which preside over this occlusion of the glottis during deglutition are not the same as those which govern its respiratory movements; they are the filaments from the spinal accessory nerve, whose influence here, as in all its other functions, is *opposed* to that of the pneumogastric nerve (Cl. Bernard).

A very important part of the physiology of deglutition is the way in which it is directed by the nervous system: deglutition is one of the most striking examples of reflex influence. We cannot simply swallow, without giving rise to a local excitation, which serves as a point of departure of the reflex action: there must be some substance in the mouth, a small portion of food or of saliva; and, when we fancy that we are swallowing nothing, the movement is really for

the purpose of conveying the drops of saliva into the throat, where their presence excites the reflex action. The will is likewise powerless to prevent deglutition, which latter continues, even if a body dangerous to life is brought in contact with this region. Finally, the most remarkable fact is that the act of swallowing must begin at the beginning: if the food be stopped in its course, it can continue only by means of a fresh movement of deglutition, commencing at the isthmus of the fauces.

The spinal cord is the centre of these nervous phenomena whose centripetal organs are the sensory branches of the trigeminus, the glosso-pharyngeal, and the superior laryngeal nerves; the centrifugal nerves are the motor branches of the glosso-pharyngeal, and the pneumogastric nerves, re-enforced by anastomoses with the facial and the spinal nerve.

The will being powerless to produce this phenomenon, we see that the brain has no share in it: thus the act of swallowing may be excited in persons under the influence of narcotics, or in animals whose brain has been removed.

The region of the isthmus of the fauces may also be the centre of anti-peristaltic movements, accompanied by disagreeable sensations (disgust) and causing vomiting (nausea); for this reason the glosso-pharyngeal nerve, which appears to be the special conductor of the sensations, is sometimes called the *nerve of nausea.*

The normal execution of the reflex action of deglutition also appears to require that the epithelium of the isthmus of the fauces shall be in a sound state. This epithelium often suffers from atrophy, and, on account of this, the sensibility of the part is impaired, and the reflex action consequently rendered difficult or impossible, from failure of the impression which gives rise to it: this is the reason that, in chronic diseases, we see persons die — or, rather, let themselves die — of hunger, because the act of swallowing has become too painful.

The epithelium of the sub-diaphragmatic portion of the digestive canal is generally of great importance in pathology: in some cases of disease it thickens and falls off, causing the furred coating of the mouth. This abnormal growth is only an exaggeration of what takes place in a normal condition in certain parts, in the tonsil, for instance. The base of this organ is formed of elements similar to those of the lymphatic follicles; but numerous prolongations in *culs-de-sac* proceed to it from the buccal epithelium, making its structure spongy,

similar to that of a gland: these prolongations are filled with epithelial detritus, the odor of which is often very offensive.

The epithelium of the remaining portions of the buccal cavity is simple, but not less important on that account. We shall find that it forms a considerable part of the structure of the papillæ of the tongue, the organs of the sense of taste. It is this which, when covered with calcareous substances, changes into *enamel*, a layer of prismatic elements forming a resisting covering for the surface of the teeth; and, by a similar transformation, produces *whalebone* or *fins* in the young cetaceans. Finally, we have seen that the salivary glands are the seat of deep and more or less considerable growths of this epithelium.

III. Sub-diaphragmatic Portion of the Digestive Tube.

The sub-diaphragmatic part of the digestive tube proceeds from the *internal* or *mucous* fold of the blastoderm by means of the envelopment which the body of the embryo undergoes

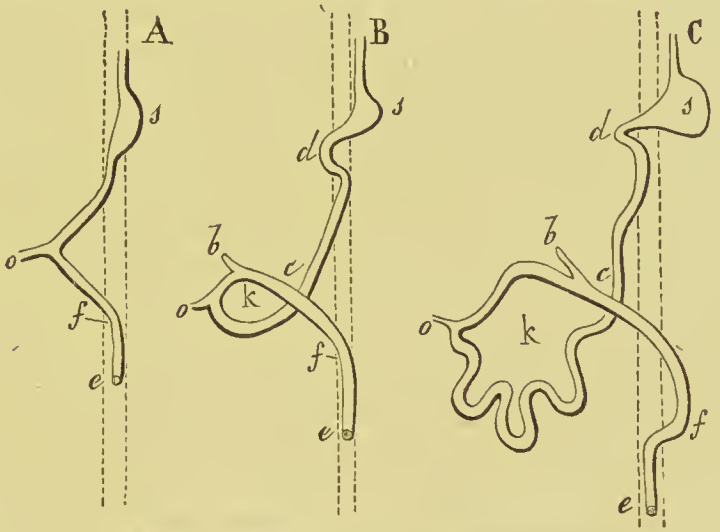


Fig. 64. — Formation of the intestinal tube.*

at the two extremities and at the sides. Its primitive cavity is divided in two: on the one side the *umbilical vesicle* (see farther on, *Embryology*), and on the other a middle tube,

* A, B, C, Different degrees of development of the stomach and of the convolutions of the intestine, properly so called. *s*, Stomach. *f*, S iliac. *o*, Omphalo-mesenteric tube. *b*, Pouch from which the cæcum is afterwards formed. *c*, Colon. *k*, Convolutions of the small intestine.

which is at first cylindrical and of an uniform calibre (Fig. 64, A). The upper part of this intestine, however, soon dilates (Fig. 64, A, *s*), and then becomes oblique; so that its lower extremity, which is the least dilated (Fig. 64, B, *d*), is turned to the right, while the left side becomes anterior. The *stomach* is thus formed (Fig. 64, C, *s*, *d*), and in the same way the pneumogastric nerve becomes anterior as it passes below the diaphragm. The rest of the digestive tube lengthens out, and, consequently, is separated from the vertebral column, and forms a loop: the tube, by means of which the intestine communicates with the umbilical vesicle, begins at the summit of this loop (Fig. 64, B, *o*). The upper branch of the loop is placed anteriorly, and soon exhibits a slight swelling (*b*), which is the first appearance of the *cæcum* and of the *cæcal appendix:* the remaining portion of the loop forms the *large intestine*, as far as the sigmoid flexure of the colon (Fig. 64, B, *b*, *f*, and C, *b*, *f*, *c*); while the convolutions of the summit and postero-inferior portion of the loop are developed (Fig. 64, B, *k*), and form the *small intestine* (C, *k*).[1]

The epithelium of this part of the digestive tube is columnar throughout, and is continued at its two extremities with the pavement epitheliums of the œsophagus and of the skin. It also forms outgrowths on the surface (or *phanères*) and in the deeper tissues (or *crypts*). The former are represented by the *villosities*, which we shall study in regard to the subject of absorption; the latter are the various glands of the intestinal tube. Some of these glands are extremely simple, as the follicles or glands of Lieberkühn, which are only a depression like the finger of a glove (Fig. 65), and are found throughout this portion of the alimentary canal; in the stomach, however, some of these depressions have a complex structure, and the epithelium of their cæcal extremity is no longer columnar; we have also the *peptic glands*. Farther on, a still more complex growth gives us glands in clusters, such as *the glands of Brunner*, in the duodenum: the *pancreas* is only a huge gland of this class. Finally, embryology shows us that the liver is itself formed of pouches similar to those of the glands of Lieberkühn, but very long, and so spacious that between them is found another glandular organ, arising from the growth of the coats of the

[1] See K. Vierordt, "Grundriss der Physiologie des Menschen." Francfort, 1860, p. 420.

omphalo-mesenteric vein (later becoming the *portal vein*). The liver is thus formed by the junction of two organs: first, the *biliary liver*, formed of tubes lined with a columnar epithelium, such as the glands of Lieberkühn; and, second, the *blood liver*, constituted by the real *acini* of the liver (around which are placed the biliary *culs-de-sac*); the purpose of these is to elaborate the blood, and especially to introduce into it sugar or glycogenous matter; whence the name of glycogenic liver, though the presence of sugar is not peculiar to the tissue of the liver.

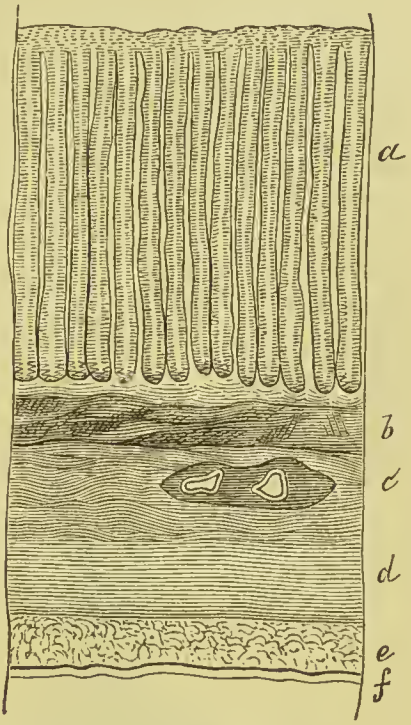


Fig. 65.—Tube-shaped glands of the intestinal mucous.*

These different glands pour into the intestinal tube their secretory products, which thus come generally in contact with the alimentary substances received from without: these substances are modified by the fluids, and at the same time subjected to phenomena of transportation (peristaltic movements) by means of the muscular coats of the stomach and intestines. We shall study these chemical and mechanical phenomena in the *stomach* and in the *intestine*, and shall see how the larger portion of the substances which are thus elaborated is *absorbed* by the coats of the digestive tube, and especially by its epithelium; and also, finally, how the residuum of the aliments, as well as the products of intestinal desquamation, are rejected after passing through the *large intestine*.

A. *Stomach.*

The *stomach* is a pouch intended as a temporary receptacle for the aliments introduced into it by the act of deglutition. Some aliments only pass through the stomach, such as, in horses especially, those fluids which accumulate in the intes-

* *a*, Thick layer of glands. *b*, Tissue belonging to the mucous and the cellular layer. *c*, Sub-mucous tissue traversed by the vessels cut transversely. *d*, Layer of the circular muscular fibres. *e*, Longitudinal fibres. *f*, Peritoneal envelope. (Kölliker, "Histologie.")

tine. Other aliments generally remain for some time in the stomach, and the length of this period is determined by the degree of difficulty which the stomach has in digesting them; those aliments which it cannot attack remaining in its cavity as long as possible.

We have to consider in the stomach: on the one hand, the *motor element* peculiarity: and, on the other, the *secretory* or *epithelial* peculiarity.

I. The motory apparatus consists of a somewhat slight fleshy tunic, which rarely contracts, and is incapable of any great exertion, at least in man and in the mammifera. Those peristaltic contractions which, by means of a sort of deglutition, carry the contents of the stomach from the cardia to the pylorus, and thence into the intestine, are extremely gentle and slow; since this kind of deglutition of bodies which

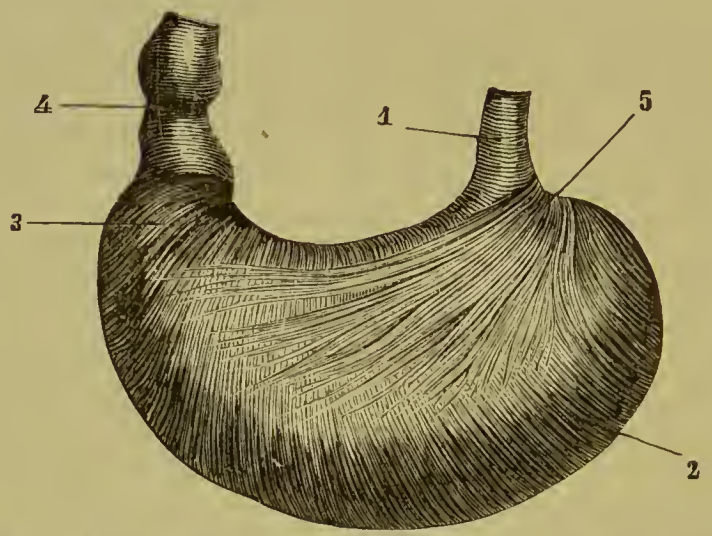


Fig. 66. — Muscular (oblique) fibres of the stomach (*cravate de suisse*) *

are sharp, hard, and apparently injurious, has been known to take place without being followed by any bad consequences. These contractions are the result of a reflex action succeeding the impression made upon the surface of the stomach by the substances received, and appear thus to make a sort of selection of those which are to remain a longer or shorter time in the stomach. Thus fluids do not accumulate in this reservoir, even during a meal, and no very great difference is

* The stomach appears turned over, and the muscular bands are shown by the removal of the mucous coat. 1, Circular fibres of the œsophagus. 2, 3, Circular fibres of the stomach. 5, *Cravate de suisse.*

found to exist between the stomach of a person who has drunk and that of one who has not drunk while eating. This is because along the anterior and posterior surfaces of the stomach there run longitudinal fibres parallel to the smaller curvature, situated at some distance from it, and extending from one surface to the other, below the cardia and the pylorus (Fig. 66). They thus form a sort of elliptical ring (*cravate de suisse*) or sphincter, which, as it contracts, divides the stomach in two parts (Fig. 67): namely, the region of the greater curvature (Fig. 67, S), hermetically closed: and the region of the smaller curvature, forming a tube which leads from the cardia to the pylorus; this canal (Fig. 67, L) is formed at the time of the deglutition of fluids, and these follow it; so that deglutition may be said to continue from the pharynx down to the duodenum without their properly entering the stomach at all.[1] Thus, in a person presenting an abnormal communication of the duodenum with the colon, the ingestion of a glass of water has been observed to

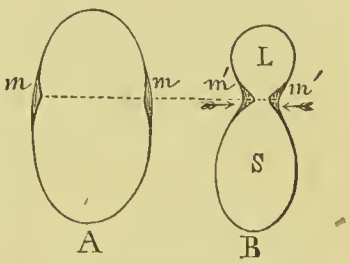


Fig. 67.—Appearance caused by the contraction of the band (*cravate de suisse*).*

[1] See R. Larger, "Essai Critique et Expérimental sur les Museles Lisses en général et sur quelques-uns en partieulier (Estomac). Thèse de Strasbourg, 1870, No. 262.

P. 59: "We have had the good fortune to witness the eontraction of the oblique fibres of the stomach, whieh we have never sueeeeded in producing artifieially. The animal was a dog. We found a tolerably deep groove, extending from the eardia to the bend of the stomaeh, exactly in the path of the oblique fibres (*cravate de suisse*); and, singularly enough, at the same time the smaller curvature of the stomach eurved outwards in a most remarkable manner. This eondition lasted for some time, and then gradually ceased, but a few moments later the same phenomenon was reprodueed. Another remarkable feature eonsists in the relaxation of the cireular fibres in that part situated above the band of oblique fibres during the eontraetion of the lower part. The tube whieh we saw formed was not eomplete in one respeet, that is, the two surfaees of the stomaeh were not united below under the influenee of the eontraetion of the oblique fibres. *The*

* A, Vertical section of the stomach in the state of repose. *m*, *m*, *Cravate de suisse.*

B, Contraction of these muscular bundles (*m*, *m*), drawing together the corresponding parts of the coat of the stomach, in the direction indicated by the arrows, and thus dividing the cavity into two parts (S and L).

be instantly followed by liquid stools, the water which enters the great intestine directly after being swallowed producing the effect of an injection.

Vomiting. — Apart from this peculiar function of the muscular *necklace* or band placed along the smaller curvature, the mechanical *rôle* of the muscular coats is, as we have said, of little importance. Thus, the stomach takes scarcely any part in the movements of regurgitation made in vomiting: it rejects its contents under the influence of the pressure exercised by the diaphragm and the muscles of the abdominal coats. Recent investigations by Schiff, however, show that if the muscular coat or tunic of the stomach does not produce the *effort* of vomiting, in order to throw off the contents of the viscera, it at least serves to aid in this rejection. To this end the longitudinal fibres of the cardiac region contract, and then, straightening their curve, distend the corresponding orifice. The attempt to vomit succeeds only when the *abdominal* pressure takes place simultaneously with this dilatation of the cardia. The pneumo-gastric nerve regulates the association of these movements.[1]

Vomiting is a reflex action resembling that of sneezing. (See p. 47.) The agents by which it is excited act upon the nerve centres either directly, or by the intervention of various sensory nerves, as the pneumo-gastric and the glosso-pharyngeal nerves. Those which act by means of this latter nerve, are called *nauseous* (see sense of taste; the glosso-pharyngeal a nauseous nerve) the rest are *simply vomitive.*

II. The columnar epithelium of the stomach exerts a protecting influence over this viscus: and prevents it from digesting itself; but, if the epithelium be injured in any part, the gastric juice acts upon the subjacent parts of the coats of the stomach, producing an erosion known in pathology under the name of *round ulcer.* The epithelium is here, as

fluids, however, could pass with the greatest ease from the pylorus to the cardia, or inversely, without mingling with the aliments contained in the cardiac portion, the latter being strongly pressed against its contents, which it thus prevented from passing out, or from being penetrated by the fluids.

"This fact justifies the hypothesis set forth by Luschka, and by Professor Küss in his lectures, which attributes to the oblique fibres, in certain cases, the power of establishing a direct communication between the orifices of the cardia and the pylorus."

[1] M. Schiff, "Leçons sur la Physiologie de la Digestion." 1867, Vol. II., 37th leçon.

on so many other surfaces (the bladder, for instance), an obstacle to absorption; indeed, it has been demonstrated that, in spite of its lymphatic and blood vessels, the stomach does not absorb. Experiments have been made, proving that a horse, in which the pylorus has been tied, is not poisoned by the ingestion of a considerable dose of strychnine (experiments by Bouley),[1] and this fact has been found to be similar in regard to man. Thus a case has been known in which a man, suffering from obstruction of the pylorus, experienced constant thirst, in spite of having swallowed large quantities of water; it was shown by an autopsy that the mucous membrane of the stomach was in a perfectly healthy condition; here thirst was relieved by the injection of water into the rectum. In the case of another patient, we have seen the ingestion of opium fail entirely of its usual calming effect, because some unknown cause prevented the drug passing out by the pyloric orifice; in this case a large quantity of opium was administered, and the obstruction at the pylorus being in some way suddenly removed, symptoms of poisoning followed, owing to the large quantity of opium accumulated in the stomach, which was afterwards absorbed in the intestinal canal.[2]

[1] Bouley, "Bulletin de l'Académie de Médecine." 1842, Vol. XVII.

[2] The question of absorption by the stomach has been, however, revived by recent investigations. Several Italian physiologists, on repeating Boulcy's experiments, have observed, like him, that in the horse large doses of strychnine introduced into the stomach, the pylorus having been previously tied, do not produce poisoning. But a new and important observation has been made, namely, that neither does poisoning take place, if, after a considerable interval, the ligature be untied, and free course allowed to the contents of the stomach. According to Schiff, this latter circumstance indicates that the absorption of the strychnine has been sufficiently gradual to allow of its being proportionally eliminated by the urine, without accumulating in the blood to such an extent as to produce poisoning. The same has been observed with woorara, which is also absorbed by the intestine, but so slowly that it is eliminated by the kidneys before a quantity which could prove fatal has had time to accumulate in the organism (Cl. Bernard). For further details on this subject, see the recent publication by F. Lussana: "Sulla Piccola Circolazione Entéro-cpatica," etc. Lo Sperimentale, Octobre, 1872. — Analyzed in "Revue des Sciences Médicales," de G. Hayem, Vol. I., p. 32.

Schiff, relying on various experiments made by himself and by Colin, admits absorption by the stomach as a general fact. We

The principal function of the epithelium of the stomach is to throw out the products of secretion. In the first place, this mucous coat, like all the others, supplies *mucus* by desquamation: this is generally found in flakes, because the shedding of the epithelial cells is not complete; but it appears only in morbid, or, at least, abnormal cases, the normal *gastric juice* containing no mucus: those glands of the stomach (identical with Lieberkühn's glands) which have been called *mucous glands*, have thus been incorrectly named, the mucus not being a normal product, and no special gland being needed to produce it. Since it is the result of desquamation of the entire free surface.

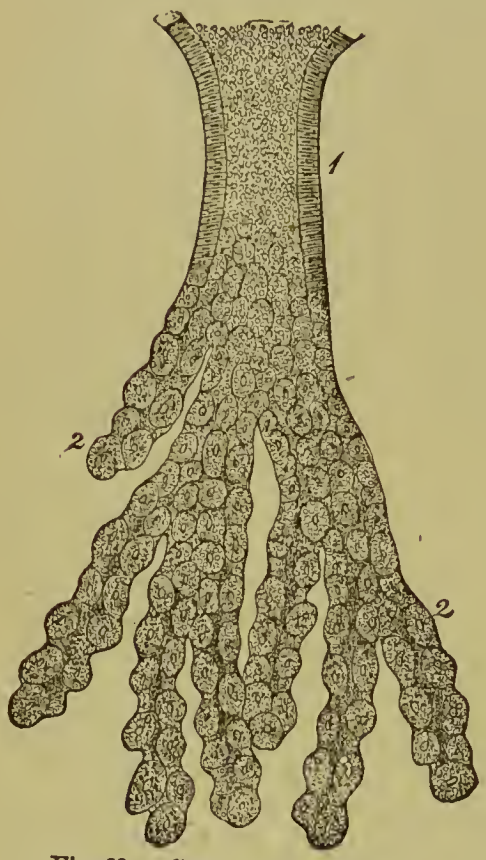


Fig. 68. — Compound peptic gland.*

The normal and characteristic secretion of the stomach is the gastric juice, which is chiefly produced by the glandular *culs-de-sac* of the cardiac region. These are distinguished from the ordinary glands of Lieberkühn (Fig. 65) by their epithelium not being columnar, but polyhedral, at least in the deeper portions (Fig. 68).[1] This gastric juice, produced by the shedding or falling off from these cellular elements, is a very tenuous fluid, containing scarcely four per cent of solid matter, two-thirds of which consist of organic substances

shall see that such absorption is neeessary to his theory of peptogenous substances, which we shall examine later.

[1] Large quantities of *closed follicles* (resembling those of the intestine) recently have been presumably discovered in the stomach,

* 1, Excretory tube, lined with a columnar epithelium resembling that of the gastric mucous in general. 2, *Culs de sac* like the finger of a glove, filled with large granular globules (cells of peptic secretion), the fragments of which are thrown upon the gastric surface by the excretory tube which is filled with them. (Kolliker.)

(albuminoids). The salts chiefly found in it are phosphate of soda, and chloride of sodium.

In order to study the properties of the gastric juice, this fluid is procured through a *fistulous* opening in the stomach, generally of a dog. Blondlot, of Nancy,[1] was the first to employ this method, which has since yielded such valuable results in the hands of Cl. Bernard and Schiff.

The organic (albuminoid) matter contained in the gastric juice is a sort of ferment called *pepsin* or *gasterase:* this ferment is of a soluble nature, like that of the saliva (ptyaline). Its existence was first pointed out by Schwann; Payen obtained it by precipitation from the gastric juice by alcohol; in this way, pure pepsin may be produced, presenting, after desiccation, the appearance of a white powder: it is often adulterated for purposes of trade by being mixed with starch. Pepsin exhibits all the reactions of albuminoid substances, though its albuminoid nature (Brucke), as well as that of ptyaline (Cohnheim), has been denied. (See Ritter, *op. cit.*). It acts on the albuminoid substances of aliments by transforming them into *albuminose* or *peptone*, which is an isomeric form of albumen, and can neither be precipitated by heat nor by acids, and is readily absorbed.

The presence of an acid is necessary for this transformation, which essentially constitutes the digestive function of the stomach; in the gastric juice therefore pepsin is united with an acid in a free state; the exact nature of this acid has been much disputed, but it has been proved by artificial digestion that, whatever it may be, the effect produced by it is always the same. Some maintain that in the normal gastric juice, this element is represented by *hydrochloric acid* (Prout, Schmidt, Mulder, Brinton, Rouget, Ritter, etc.); others, by *phosphoric acid* (acid phosphate of lime, Blondlot); and others still, by *lactic acid* (Cl. Bernard, Barreswill): the latter opinion is now most generally held.

It must be admitted that the arguments which have decided physiologists in favor of the existence of different acids have all some foundation, but may all be more or less completely refuted, and that organic chemistry seems, up to

especially about the region of the pylorus. Sappey has, however, shown that these supposed closed follicles are only tubular glands, of which the excretory canal is obliterated, and which develop in the form of a small spherical cyst. (See "Anat. Descriptive," Vol. IV., p. 187.)

[1] Blondlot, "Traité Analytique de la Digestion." 1843.

this time, to be powerless to dispel all doubts on the subject. Blondlot's acid phosphate of lime appears really to exist in the gastric juice, that is in the gastric juice of dogs that have been fed on bones; it is thus only the remains of former digestion. The same objection may be made in regard to lactic acid: indeed if lactate of zinc be obtained by the action of the gastric juice upon that metal, the lactic acid which is then observed is often, perhaps, only the remains of previous digestion. On the other hand, it is quite possible that hydrochloric acid, the presence of which is incontestably proved by chemical reactions, may arise from decomposition of the chlorides by the lactates: "a mixture of albumen and chloride of sodium is coagulated by lactic acid: as neither chloride of sodium nor lactic acid of itself produces this effect, the coagulation can only be attributed to hydrochloric acid which is produced by double decomposition." (Cailliot. Thèse by Ritter). The best arguments that can be adduced in favor of the presence of hydrochloric acid are the following: elementary analysis of the gastric juice reveals more chlorine than is requisite to saturate the soda found in it: there must therefore be some chlorine in the form of hydrochloric acid; so long as the chlorine remains in the gastric juice, the soda of the chloride of sodium remains in the blood, whence the increase of alkalinity in the blood, and to such a degree that the urine, which in its normal condition is acid, becomes alkaline during energetic digestion (Brinton, Bence Jones). On the other hand, Schiff has shown that the introduction of dissolved dextrine, by the veins or the rectum, promotes digestion by the stomach, the acidity of the gastric juice being increased. If this fact be true, the acid thus obtained in a larger quantity can only be the lactic acid.

The flavor and the acid reaction of the gastric juice have, however, been greatly exaggerated: in pathological cases this acidity increases; but in the normal condition it is so slight as not to be sensible to the taste. The acid smell of the substances thrown off by the stomach arises from decomposition of its contents: indeed, under certain circumstances, fatty volatile acids may be formed in it (butyric acid). These properties show that the gastric juice does not constitute a mucous or a glairy acid, as was supposed, but a peculiar fluid analogous to and comparable with the saliva.

In order to complete the subject of the products given off in the stomach, we must add that this organ, as well as the

rest of the intestinal tube, produces gases in considerable quantity; chiefly carbonic acid and nitrogen. Thus these do not always arise from fermentation but really come from the blood, and are evolved, for instance in all cases of paralysis of the digestive tube, whether or not it contains alimentary substances; they may thus be suddenly produced under the influence of moral emotions, and be as quickly reabsorbed.

Cl. Benard has recently called the attention of physiologists to similar facts. "In the lung," he says, "and on the cutaneous surface, these gases may be exhaled simply as a result of simple interchange between the exterior and the interior medium; but in the intestine, in which normally no air exists, the exhalation of gas must take place by means of a different mechanism. The nervous system has, probably, some influence in producing these gases, for I have known them to appear in large quantities after operations performed upon the spinal cord. The eliminated gaseous substances are generally those which can be absorbed. Hydrogen, however, which is not sensibly absorbed, is sometimes exhaled in various quantities, as shown in experiments by Regnault and Reiset." [1]

The conditions under which the fluids of the stomach are secreted are quite peculiar. Thus mucus is readily produced when the stomach is fasting or fatigued, or when occupied by a foreign body which is not alimentary; a sponge, introduced into the stomach, imbibes a mucus which is sometimes strongly acid (gastric juice without pepsin) and must not be confounded with the real gastric juice, as was formerly done.

The real gastric juice is secreted only under the influence of an excitant of a peculiar character, an alimentary substance; or, in other words, secretion takes place chiefly when the aliment is an albuminoid (muscular flesh, fibrine, white of egg), that is to say an aliment which essentially requires the action of the gastric juice. Under these circumstances the coat of the stomach in all those parts which come in contact with a suitable excitant, becomes red and turgescent, and there ensues an abundant secretion of the gastric juice, which soon transforms the albuminoid aliment into albuminose. These facts show that the secretion of the gastric

[1] Cl. Benard, "De la Physiologie Générale." Notes, p. 290, 1872.

juice is the result of a *special sensibility* on the part of the mucous of the stomach, and that this delicate sensibility cannot be deceived: an aliment suitable to digestion by means of the gastric juice is needed to produce it. The mucus, on the contrary, is secreted when the stomach craves food, or is occupied by a foreign body, which the mucus surrounds and isolates.

It has also been ascertained that after section of the pneumogastric nerves, the gastric juice is still formed, though in smaller quantity: the nerves are not, therefore, indispensable to the act of digestion; the great sympathetic nerve is generally considered as regulating the digestion of the stomach.

That remarkable peculiarity by which the secretory organs of the stomach yield genuine gastric juice only when in contact with certain alimentary substances, is now fully recognized, but ought not, perhaps, to be attributed to a peculiar *sensibility*, to a sort of *intuition* (Blondlot) of the stomach; but rather, according to Lucien Corvisart and Schiff, to the fact that these substances furnish an indispensable element in the secretion of pepsin: this is the theory of the *peptogenous substances* and *peptogeny* of Schiff, a theory which has already produced many practical results, and which we will here sketch rapidly.

Schiff has proved by numerous experiments that pepsin is not formed uninterruptedly in the peptic glands, simply by the nutrition of the coats of the stomach; but that a stomach fasting and *exhausted* by copious digestion loses the property of yielding a gastric juice which is really active, until, having absorbed certain substances, the coats of the stomach become ladened with elements which are capable of being changed into pepsin: these substances are called *peptogens*. Thus, after the exhaustion produced by copious digestion continuing from twelve to twenty-four hours, the empty stomach nearly loses its power of digesting the albumen; but this power increases in a remarkable degree, if a moderate quantity of other aliments (*peptogens*) be introduced into it along with the albumen. In this case, the stomach first secretes a purely acid fluid, which serves to dissolve the peptogenous elements; and as these become absorbed, and, mixing with the blood, enable it to furnish pepsin to the glands of the stomach, we observe that the secretion of a gastric juice becomes constantly more active or, in short, peptic. These peptogens are essentially represented by the elements

of meat which are soluble in water, by gelatine and by dextrine: broth and soup thus contain a large quantity of peptogenous matter, and our every day experience in this respect agrees perfectly with the latest scientific *data*.

These peptogens appear to be absorbed by the stomach, but their action would be precisely the same, if they were introduced into the organism by being injected into the subcutaneous cellular tissue, into the rectum, or directly into the veins. It is remarkable that when absorbed by the small intestine, these peptogens entirely lose their power; not because of any change produced in them by the intestinal canal, by the bile or the pancreatic juice; but because, being absorbed by the chyle ducts, they cease to be peptogens, in passing through the mesenteric glands. It must be admitted that Schiff's researches on this latter point have not the precision which marks the earlier part of his series of investigations; and that it is hardly possible to believe all the experiments the aim of which is to show the action of the mesenteric ganglions; but the question of absorption by the stomach and of the uselessness of intestinal absorption, does not, in spite of the apparent paradox, at all diminish the general importance of the theory of peptogeny, as a question of pure physiology, and as the fruitful source of therapeutical applications.

It was, indeed, to be supposed, *à priori*, that, in many genuine cases of dyspepsia, that is, sluggishness of the digestive organs; occasioned by insufficiency of the gastric juice secreted by the stomach, the derangement might be simply owing to the peptic glands not finding in the blood the materials necessary to *impregnate* them sufficiently. What this disease requires, therefore, is simply an artificial increase of the peptogenous substance contained in the blood, and it is simply necessary, as in physiological experiments, to *prepare* the stomach, by impregnating it beforehand with a sufficient quantity of peptogens and, consequently, of pepsin, in order that the work of digestion may begin as soon as food is received. Schiff mentions the case of some persons suffering from this malady, who were cured in a few days by taking *soup* an hour or two before a meal, or a draught of a solution of dextrine, or even an injection of the same, half-an-hour or an hour before taking food.

We know that food consists of albuminoid substances, of feculent or saccharine substances, and, finally, of fatty matters. The gastric juice is not known to have any effect upon

these fatty matters. The amylaceous substances are changed into dextrine, and saccharized in the stomach, by means of the saliva which is swallowed with the food. The quantity of saliva varies according to the continuation of mastication a longer or a shorter time: thus when the digestion is impeded, a larger or smaller quantity of saliva is finally swallowed, and this assists the action of that which was swallowed with the food. This helps us to understand the difficulty, in artificial digestion, of operating upon the gastric juice alone, or unmixed with saliva.

The albuminoid substances, finally, belong essentially to the province of the gastric juice, and to that alone (we are not now speaking of the intestinal juices). If a piece of muscular flesh be placed in contact with the saliva, it quickly putrefies; while if the same experiment be made with the gastric juice, the meat is preserved, and even putrefaction, which has already begun, arrested. The saliva thus evidently has no effect upon this class of aliments. The property possessed by the gastric juice of arresting decomposition was first observed by Spallanzani, and several surgeons have attempted to make use of it, in arresting the putrefaction of wounds. The odor of the stomach of those animals which feed on carrion is not more powerful than that of others, even after the ingestion of meat which is very strongly tainted.

The most remarkable effect produced on albuminoid substances by the gastric juice is the transformation which they undergo. Those which are fluid are changed into another fluid, more absorbable, and which does not coagulate under ordinary reactions. Thus the white of egg, when mixed with the gastric juice, becomes fluid like water. Casein alone, when brought into contact with the gastric juice, coagulates before disappearing: this property is made use of in curdling milk, by means of the pepsin contained in the preserved stomach of a calf (*rennet*).

The solid albuminoid substances, either before ingestion, or when coagulated by pepsin, like casein, are liquefied by the gastric juice. To this process there are two stages. The albuminoid substance, a small cube of the white of egg, for instance, first swells; its edges then lose their regular outline, and it is finally reduced to a tenuous powder: in the first stage, no part is really dissolved; such porphyration or crumbling occurs as would be produced by mechanical action, and yet it is simply owing to the action of the gastric

juice. The paste thus obtained is not the final product of digestion; it is what was formerly called *chyme*, before the action of the gastric juice had been so minutely studied as at present. This first stage is, however, followed by a second, in which this pulp becomes completely liquefied; and it is under this form only that the products of digestion pass from the stomach into the intestine.

This *porphyration* and succeeding liquefaction are accompanied by changes of color in the digested substances: thus the white of the albumen of an egg becomes slightly yellow or even red; during the first stage blood becomes quite black (vomiting of half-digested blood, in hemorrhage of the stomach: black hæmatemesis); it is afterwards resolved into a nearly colorless fluid. The final product of digestion by the stomach is usually slightly yellowish. These changes in color should be well known in order to avoid mistakes as to the nature of the substances vomited.

The final result of these different processes is the production of new kinds of albumen, *peptones* or *albuminoses*, which are, as we have said, especially suited for absorption. The peptones always preserve some feature of their original substance: they are found in the white of egg, in collagenous tissue, in fibrine, etc. The length of time necessary for this transformation depends on the nature of the aliments: thus the white of egg is digested sooner when raw than when cooked; raw, or at least partially cooked, meat, is generally much the easiest to digest, and should therefore be preferred (setting aside the question of the entozoa).

The study of the *peptones* or *albuminoses* is one of those which have made the most progress of late years, owing to the researches of Lehmann, Brücke, Meissner, Mulder, Schiff, etc. It has been discovered, in the first place, that the *perfect peptone* is a remarkably assimilable and endosmotic product: its chief characteristic in a physiological point of view is, that, if it be injected directly into the veins, it does not reappear in the urine, showing that it is immediately assimilated by the tissues. Chemically considered, it can be precipitated neither by heat, acids, nor alkalies, but solely by bichloride of mercury, Millon's reagent (nitrous or acid nitrate of mercury) and some other rare reagents. The real peptone thus consists of albumen which is not only *dissolved*, but also *transformed* (chiefly by *hydration*, according to Brinton).

The real definite peptone is not, however, produced in the

first place by the action of the gastric juice; in the series of processes which we have described (porphyration, liquefaction, change of color), a series of decompositions occur, producing tolerably well-defined intermediate peptones; such as the dyspeptone, the parapeptone, the metapeptone, and, finally, the definite peptone.

The *dyspeptone* is the residuum of digestion of the casein; it is quite insoluble, and cannot be assimilated. The characteristic of the *parapeptone* is that it is precipitated by neutralizing its acid solution; the metapeptone, on the contrary, is precipitated by increasing the acidity of the product of the stomach, and definitively by concentrated mineral acids. These forms are only transitory, and as the digestion approaches its termination, they have all a tendency to change into genuine peptones, with the exception of the dyspeptone which remains in its former state, and of the parapeptone, which shows a tendency to change into the same. Some less important forms of transition have been observed between the *metapeptone* and the *definite peptone* (peptone A, peptone B), which are principally produced during the digestion of the fibrine (Meissner, De Bary, Thiry).

These transformations, especially the definite peptone, are owing to the combined influence of the acid and the pepsin of the gastric juice: these two elements of the digestive fluid must act together. For instance, it would be useless to operate on meat with hydrochloric acid, and then, after complete washing, to place it under the influence of a solution of pepsin: in this case no peptones would be formed; the albumen only would be more or less entirely dissolved. On the other hand, if pepsin and any acid ($\frac{1}{1000}$ to $\frac{4}{1000}$ in solution) be employed simultaneously, we can produce *in vitro* artificial digestion, yielding nearly the same results as natural digestion.

The production of the real peptones must not be supposed, however, to be one of those processes of transformation to which the organism alone, or some growth (pepsin) borrowed from the organism, can give rise. This transformation, like all the chemical transformations which we see taking place in plants and in animals, shows no such monopoly of power as theorists of all ages have agreed in attributing to the agents of life. Peptones may be artificially produced, but the process is long, and more curious than practical. Meissner obtained perfect peptones from muscular flesh, with casein, legumin, etc. (*albuminose by boiling,*

E. Corvisart), by long decoction in Papin's digester; the same process with white of egg yields metapeptone, which may be afterwards transformed by the stomach or by artificial gastric juice into genuine peptones. Peptones have also been produced by the action of ozone on the albumen of an egg and on casein (Gorup-Besanez, Schiff), but for this purpose the ozonized air must be made to pass during sixteen to twenty days through a solution of albumen and water; and this process, after all, yields only products resembling peptones; if injected into the veins of an animal, some of them will reappear in the urine (Schiff).[1]

If we study the phenomenon of gastric digestion as a whole, we no longer find in it, element by element, the simple action which we have been examining: we know that the amylaceous substances continue to be transformed into sugar by the action of the saliva. The fats become slightly emulsive under the influence of the motions of the stomach, and by mingling with the porphyrized product of the solid albuminoids; but this emulsion is extremely unstable, and the drops of fat show a tendency to reunite in large masses, which float on the surface of the liquid. The different albumens are transformed into different *peptones*, but there are some kinds which for a long time resist the action of the gastric juice: such as the cellular tissue of the muscles: and some, finally, as the cellulose of plants, which are almost refractory. The mingling of these different substances with a large quantity of gastric juice forms what has also been called *chyme*. But we see here, too, that the *chyme* is not a substance immediately formed, but an extremely complex pulp, and not at all fitted to give an exact idea of the digestive action of the stomach.

Attempts have been made to decide on the quantity of gastric juice necessary to dissolve an aliment. In artificial digestion a large quantity is required: thus one part of concrete albumen requires twenty-five parts of the juice; the quantity secreted is, therefore, very abundant, and is estimated by litres: in man, for instance, it may be twenty litres in twenty-four hours. The usual standard in animals is one hundred grammes of gastric juice to one kilogramme of the

[1] See Cl. Bernard, "Leçons sur les Propriétés Physiologiques et les Altérations Pathologiques des Liquides de l'Organisme." Paris, 1859.

Blondlot, "De la Manière d'agir du suc Gastrique." (Gazette Medicale, 1857.)

animal's weight: this would give for man, whose mean weight is sixty-five kilogrammes, only 6500 grammes of gastric juice (in twenty-four hours).

The most moderate estimate thus places the weight of this juice at one-tenth of that of the body of the animal during the period of twenty-four hours. The case has even been cited of a woman, having a gastric fistula, and was nursing, who yet at the same time produced a quantity of gastric juice equal in weight to one quarter of that of her body (Béchamp).

B. *Small intestine.*

Intestinal Secretions and Digestion. — We are already acquainted with the epithelium of the intestinal tube, properly so called, its villosities and its glands (p. 191). We will study the villosities more completely when we come to the subject of absorption. What we have to do now is to seek to discover the nature of the fluids which flow from the glands, and which come more or less in contact with the product of the digestion of the stomach.

The contents of the stomach enter the intestine in waves, and pass very quickly through the first part of the tube; this tube has been called the *jejunum*, because it is generally found empty, the contents of the intestine accumulating in the lower part of the small intestine (*ileum*). It has been generally supposed that the secreted products of the different glands were poured into the intestine at this moment, and thus came in contact with the alimentary substances. This is the case with regard to the product of the glands of Lieberkühn, and that of the pancreas, but not of the bile. Study of biliary fistulæ proves that the bile is poured into the intestine long after the passage of the product of the stomach. The secretion of the bile is connected with absorption, not digestion, and we will study it under that head.

The fluid secreted by the glands of Lieberkühn constitutes the *enteric juice:* this juice is very difficult to collect, and, on this account, the ideas entertained respecting it were erroneous, or, at least, extremely hypothetical: Thiry's process of procuring it, which is now employed, consists in isolating a certain length of the intestinal tube by two sections; and joining the tube together again, so that the fluids may flow as before; one extremity of the part which has been detached, and which adheres only by its mesentery, is then sewed up, so as to form a pocket or *cul-de-sac*, while

the other is left open, and fastened into the open wound in the abdomen. The intestinal fluid obtained through this orifice is quite pure; it is a limpid juice, slightly yellow, very tenuous, and alkaline; its properties are nearly all negative: it acts neither on starch nor on the fats, nor yet on the albumens in general, but solely on the *fibrine of the blood*, which it changes into *peptone*. Almost the only purpose which it serves is thus to dilute the contents of the intestine.[1] The secretion of this fluid takes place by means of chemical, especially acids, or mechanical excitants, such as the presence of a foreign body. In some pathological cases it is secreted in great abundance, producing the *serous* diarrhœa which is sometimes so alarming.

Daily observation has long shown what is *the influence of the nervous system in producing the flow of the intestinal fluids*. The effect produced on the action of the intestinal tube by certain moral impressions, and the untoward increase of the fluid products, which sometimes accompanies a strong sensation of fear or of danger, is a familiar occurrence. Direct experiments on animals have shown that this is caused by reflex paralysis of the nerves of the intestine, particularly the vaso-motor nerves. If two ligatures be placed around the intestine at some distance from each other, and the nerves leading to the part included between them be cut, the veins and arteries being carefully avoided; and if then the intestine be replaced, this intestinal loop will be found on the following day distended by a considerable quantity of clear, alkaline, and very tenuous fluid, strongly resembling the enteric juice. An additional proof of the influence of the nerves consists in enclosing another intestinal loop between two ligatures, avoiding, however, the nerve threads. The mucous of this part of the intestine, instead of being saturated with fluid, is found sticky to the touch, and nearly dry, as in an intestine during fasting.[2]

The *pancreatic juice* is also called the *abdominal saliva;* as the structure of the pancreas resembles that of the salivary glands, so its secreted product closely resembles the saliva; it differs from it, however, in the proportion of solid matter, for it contains only 90 per cent of water, while the saliva contains 99 per cent. The pancreatic juice is, therefore,

[1] *Vide* Boylston Prize Essay, "On Intestinal Digestion," by G. M. Garland. D. Clapp & Son, Boston.

[2] A. Moreau, "Recherches sur la Secrétion Intestinale." (Comptes-rendus de la Société de Biologie, 1850.)

comparatively, very thick; it coagulates readily, being rich in albumen.[1] It is alkaline, like all salivas, and, when brought in contact with the product of the stomach, impregnated with the gastric juice, it neutralizes the acidity of the latter, and begins to act in its turn. By means of the ferments which it contains, it acts simultaneously on the amylaceous substances and the albuminoids: transforming the former into sugar, by the saliva, and the latter into peptone, by the gastric juice. This latter effect is different from that produced by the pepsin, inasmuch as in this case liquefaction takes place instantly, without the intermediate stage of porphyration. This juice is also allowed to possess the property of making an emulsion of the fats (Cl. Bernard), even separating some of them into glycerine and fatty acids; but the latter of these two effects appears to be produced only when the pancreatic juice is decomposed, and the former only when the fat and pancreatic juice are closely mingled together by violent agitation: as these conditions are not realized in the intestine, we must conclude that the pancreatic juice has no physiological effect upon the fats; it may also be directly ascertained by opening the body of an animal while the process of digestion is going on, that the fats are not in a state of emulsion, but are found in masses in the in-

[1] The identity of the panereas and the salivary glands, even in an anatomical point of view, is denied by Giannuzi, whose recent researches have led him to consider the pancreas as rather resembling the liver. "The excretory tubes of the panereas have very thin walls, lined inside with a columnar epithelium. They have not the same connections with the secretory vesicles as the salivary glands; but they form around them a net composed of very fine tubes, which have no epithelium, and surround the panercatic cells with their meshes. This net may be compared to that of the biliary ducts. The network of the exeretory tubes of the different vesieles, which form the same glandular lobule, have connections between them, and form a common network. The pancreatic vesieles have no coat. The pavement epithelium of the vesicles is formed of flattened cells, having a nucleus and a prolongation. In short, they are very similar to those of the salivary glands; their nucleus, however, is more easily perceived, and their protoplasm is more granular, and contains fatty granulations. The semilunar bodies in the sub-maxillary glands, described by Giannuzi, and since discovered by Kölliker, Heidenhain, and Boll, in the salivary glands, are not found in the glandular vesicles." (See p. 221, Giannuzi, "Comptes-rendus de l'Académie des Sciences.")

testine. We shall also see that this emulsion is not necessary in order to comprehend the mechanism of absorption.

The secretion of the pancreas appears to be nearly continuous, like that of the saliva; it is generally, however, very inconsiderable, but greatly increases as the product of the stomach enters the intestine. This is evidently a reflex act, though the nervous organs of this phenomenon are not yet perfectly known; it has, however, been observed that section of the pneumogastric nerves checks the secretion from the pancreas. When normally secreted, remains of the cells of glandular pouches are found in this product: according to the general law, therefore, this secretion is produced by the shedding of the glandular elements.[1]

The influences which govern the secretion of the pancreatic fluid appear to be of the same nature as those which govern the secretion of the gastric juice, and especially of the pepsin of that juice. As the stomach needs the *peptogens* (see p. 242, above), so the pancreas needs the *pancreatogens;* thus the pancreas secretes, less by means of a reflex nervous mechanism, than because at a given moment it is *impregnated* with those substances which are fitted to give rise to secretion; that is, the blood brings to it the peptones which have been already elaborated by the stomach. The theory of the pancreatogens, established by L. Corvisart, even precedes that of the peptogens, and was the starting-point of the latter.[2] It has been taken up again by Schiff, who has introduced into it some new ideas as to *the functions of the spleen in regard to digestion.* Indeed, while the stomach receives the peptogens directly from the circulation (provided that the blood contains any), the formation of the pancreatic juice requires the intervention of the spleen. After extirpation of the spleen, or a deep wound

[1] "Does the secretory cell of animals concentrate or create the direct elements which it contains? It is difficult to answer this question. For instance, I have observed that during hibernation the pancreatic cell in animals contains no pancreatine. The case is the same with fasting animals; but directly food is received and digestion begun, these cells fill with pancreatine and become active. It must be admitted here, either that the pancreatine has been formed in the gland by the nervous influence, or has been brought into it by the blood." (Cl. Bernard, "De la Physiologie Générale." Notes, 1872, p. 284.)

[2] L. Corvisart, "De la Fonction Digestive du Pancréas sur les Aliments Azotés." (Gazette Hebdomadaire, 1860.)

made in it by way of experiment, Schiff has found that the pancreatic juice, secreted at the very moment when it is generally most active, is entirely deprived of that ferment by means of which alone it can act on the albumens.

A number of experimental and clinical results here present themselves, in the midst of which it is difficult to decide on which will finally prove to be a gain to physiology; we will, however, sum them up rapidly, in order to show how much there still is to study in the digestive functions, and in the spleen, an organ which is still a mystery in every respect (see p. 206).

While injury to the spleen weakens the digestive properties of the pancreatic juice, Schiff discovered that it renders the secretion and the action of the gastric juice much more active: by taking out the stomach and the pancreas of an animal, Schiff found that artificial digestion, by means of an infusion of these tissues, yields three grammes of digested albumen for the stomach, and from thirty to fifty centigrammes for the pancreas. But if the stomach that is used be taken from a similar animal which has been previously deprived of its spleen, the artificial digestion by means of the gastric membrane will liquefy in an equal amount of time eight grammes of albumen; while that of the pancreas has no digestive effect upon the albuminoids. We see, in the latter case, that the gastric membrane alone digests a larger quantity of matter than the stomach and the pancreas together, in the case first mentioned.

According to Schiff, the increase of appetite observed in animals whose spleen has been removed, is caused by this large increase of the digestive action of the stomach, and he thus explains the case of a woman who, after extirpation of the spleen, was afflicted with an enormous appetite.

More curious facts still lead us to infer that as the pancreatic juice loses its influence over the albuminoids, its power over the fatty and the amylaceous matters becomes still greater than before. (Vulpian, "Cours du Muséum," 1866.) In order to comprehend that there is nothing unreasonable in this view, we must first call to mind that researches by Kühne, Danileski, Hoppe Seyler (Ritter, *op. cit.*), have proved that the pancreatine which is the active principle of the pancreatic juice, is a mixture of three individual ferments, having each an independent action: the first, precipitable by calcined magnesia, acts upon the fats; the second, separated by precipitation from a solution of collodion, is

the ferment of the albuminoid substances, while the third, which resembles ptyaline, is precipitated like this latter by concentrated alcohol, and acts upon the amylaceous substances. As these three active principles can be isolated, and act independently of each other, it appears, from what we have said, that the spleen has influence over the ferment of the albuminoids only, and that, moreover, the quantity and the action of the two other ferments increases in direct proportion to the diminution of the first. At least, the facts related by Vulpian appear to show this. "Is there," he asks, "any increase in the action of the pancreatic juice on the fatty substances, or are the results which I shall quote from Schiff caused solely by the greater activity of the gastric digestion? It is true that Stinstra admits (in a thesis drawn up under the direction of Van Deen) that there is a larger deposit of fat in all parts of the body in animals whose spleen has been removed; moreover, according to Schmidt, the farmers in some parts of England have a custom of extirpating the spleen of calves, in order to fatten them more rapidly."

II. *Movements of the Intestine.* — The food, having been thus modified by the enteric and the pancreatic juices, then passes through the small intestine by means of its peristaltic movements.[1] In the normal condition these movements are always slow and feeble; but, if they become exaggerated, pains known as *colicky* are produced. These contractions are reflex, and are increased chiefly in pathological cases: thus the effect of some purgatives is to increase these movements; this is the case with oils and vegetable matters generally. Saline purgatives, on the other hand, act chiefly by causing hypersecretion of the glands of Lieberkühn, and give rise to serous diarrhœa, without colic. If the body of a man who has died in good health and during digestion be examined, there will be found, at short distances in the intestinal tube, waves of alimentary matter, associated with red patches upon the mucous coat, which is colorless between these points. This state of congestion corresponds with the more active secretion that takes place at these points; the pancreas also is highly congested during secretion.

The alimentary substances seem to pass rapidly through the two upper portions of the small intestine (*duodenum*

[1] See Legros and Onimus, "Recherches Expérimentales sur les Mouvements de l'Intestin." (Journal de l'Anat. et de la Physiol., de Ch. Robin. 1869, No. de Janvier.)

and *jejunum*); but as they approach the *ileum* their progress seems slower, they begin to mingle together, and finally are found accumulated at the lower end of the small intestine. As they are subjected to *absorption* during this passage, they may be said to move more slowly in proportion as their consistency increases and their quantity diminishes.

IV. Absorption.

A. *Absorption in general, rôle of the epitheliums, function of the villosities.*

We have seen that the stomach absorbs no part of its contents, and that the phenomenon of *rejection* (*refus*) is caused by the vitality of the epithelium which lines the mucous coat. In the intestine, on the contrary, absorption takes place very rapidly, and we shall also find that the phenomenon of passage is solely dependent on the characteristic vitality of the intestinal epithelium.

Setting aside the property of the epitheliums, the phenomena of *absorption* may be generally considered as phenomena of *diffusion*. These are known to everybody. Most people have tried the experiment of pouring red wine upon water contained in a glass, pouring it so slowly as to prevent the wine mixing with the water. The colored wine is then seen to rest upon the surface of the water, the latter remaining colorless, as the wine is lighter than the water; and the two layers are so distinct that one would imagine that they could never mingle. After a short time, however, though remaining quite undisturbed, the two fluids mix, and become homogeneous; the water has passed into the wine, or is diffused into it. Something similar takes place in absorption, looked at from a general point of view. Indeed, the organism being composed of four-fifths of water to one-fifth of solid matter, may be compared to a sponge soaked in water. Now, if a sponge soaked in water be placed in alcohol, the latter will penetrate the water in its turn, intermingling with it; in this case the sponge may be left out of the account, the essential feature of the phenomenon being an act of *diffusion* between the alcohol and the water (contained in the meshes of the sponge). The fact of the circulation of the blood is only accessory. A frog may be deprived of its circulation, and yet if one of its limbs be dipped into a solution of strychnine, the poison will be diffused throughout its whole body, will reach the spinal marrow, and kill it in the convulsions

of tetanus. If the circulation still exists, these phenomena are produced much more quickly, because the motion of the blood hastens the diffusion of the poison, without, however, being indispensable to it: circulation is to absorption what the movements in breathing is to the diffusion of the gases or respiration.

The vessels cannot thus, in the proper sense of the word, be said to be absorbing organs: it is, properly speaking, the fluids of the tissues, the blood itself, which absorbs. The state of the blood has thus a great effect on the intensity of the absorption. If the blood be saturated with water, as, for instance, after an injection of water into the veins of an animal, a fresh quantity of water will not easily penetrate. Absorption is also very sluggish in the case of hydræmia; and becomes very active, on the other hand, if the mass of the blood be diminished (by bleeding), or if it has been thickened, as, for instance, by purgatives or diuretics in the case of the patients already mentioned. Similar experiments have been made in regard to absorption of the fats. If the blood is surcharged with fat (the normal proportion is 3 to 1000), the fatty substances ingested will be found nearly entire in the alvine discharges, and scarcely any will be absorbed. We may therefore say, in conclusion, that the state of saturation or non-saturation of the blood is one of those causes which have the most influence on absorption, in regard to one substance or another.

This diffusion, however, can take place only when the epithelium which forms the barrier between the organism and the fluids deposited on its surface permits and facilitates their passage: the chief point of the study of absorption is thus the attitude assumed by the intestinal epithelium during these phenomena.

In order to increase its points of contact with the matters to be absorbed, the intestinal mucous forms numerous folds, as the *valvulæ conniventes*, and especially the *villi*. These are composed of a casing of columnar cells (Fig. 68), which, as seen in front, appear as a sort of hexagonal flooring (free base of the cell), while at the summit they are inserted in the body of the villus (Fig. 69, A), and are in contact with smaller cells, polyhedral or irregular, the germs of future columnar cells (which are to these what the layer of Malpighi is to the more superficial cells of the epidermis). The central part, *or body of the villus*, is very complex (see Fig. 69, A and C). This is composed of an embryonic connective

tissue, having a large number of embryonic or plasmatic cells. In this tissue are found two vascular systems, the first being a network of blood vessels placed throughout the deeper tissues, and especially near the surface, so near that they almost touch the epithelium. The second is a central tube, the extremity of a *chyle-duct;* it terminates at the summit of the body of the villus, but in a manner at the present time unknown (see lymphatic system, p. 201, above). Some maintain that it terminates in a *cul-de-sac*, and others that it is gradually blended with the substance of the body of the villus or papilla. However this may be, the general appearance would lead to the belief that this tube is only the excretory tube of the network of blood-vessels, in the midst of which it is placed. We see thus that the blood-vessels are better fitted for absorption than the chyliferous vessels.[1]

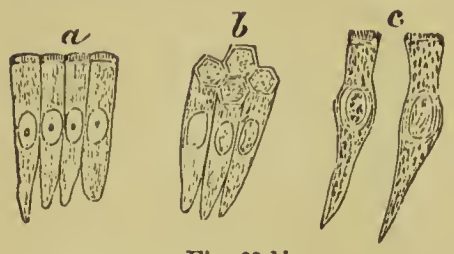


Fig. 68 *bis.*
Elements of columnar epithelium.*

When the stomach pours its contents into the small intestine, the villi, both the epithelium and the body of the villus, change their appearance as the fluid passes through. This phenomenon may be artificially produced by taking the fluid from a stomach in which digestion is going on, filtering it, and bringing it into contact with the intestinal mucous, recently taken from the body and still living. Any other substance than the contents of the stomach, that is, any element which has not been diluted with a large amount of gastric juice, would produce no effect upon the intestinal

[1] According to some recent researches by Debove ("Compt. rend. de l'Académie des Sciences." Decembre, 1872), these deep cells form an *endothelial layer*, that is to say, formed of cells identical with those which cover the serous membranes, flat cells joined together by a very fine cement: they are made visible by employing nitrate of silver. What His saw in the villi, and described as the casing of a central chyliferous vessel, would be, according to Debove, precisely the endothelial or sub-epithelial layer belonging to the surface of the villus.

* *a*, Four cells joined together, seen from the side; the free surface (at the top) shows a thick border, striped with fine striæ. *b*, Similar cells, their disengaged surface being inclined upwards and outwards: the hexagonal form of the section and the thick edge should be remarked. *c*, Cells modified and slightly distorted by imbibition, their upper edge appearing ravelled. (Virchow.)

mucous; but, on contact with this fluid, even four hours after death, the mucous becomes white and thicker and more resisting. On examining it closer, we find that these phenomena are at first only caused by changes in the epithelium. The epithelial cells, which, when the animal is fasting, are

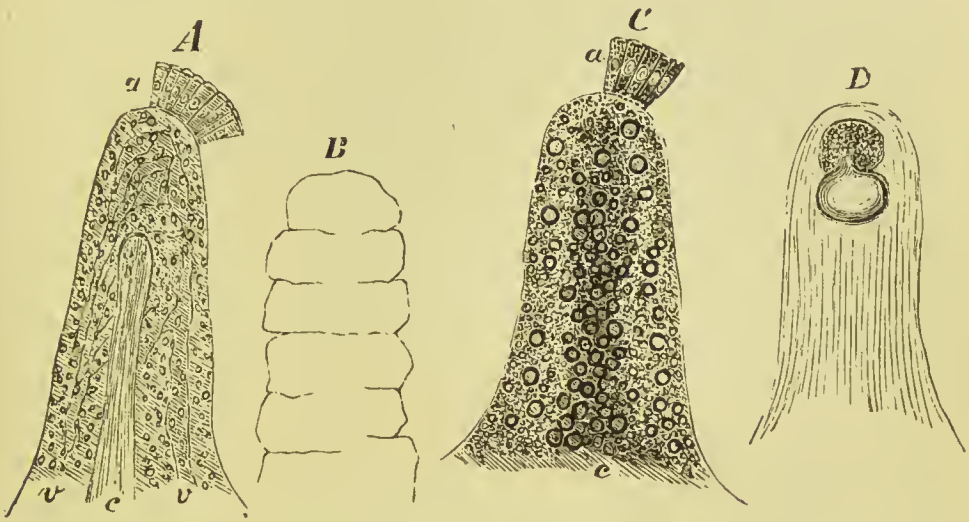


Fig. 69.—Intestinal villosities observed during absorption (especially during the absorption of fat). (Virchow.) *

small, somewhat diffluent, and hardly forming a distinct membrane, swell when excited by the gastric juice; and, as it were, standing erect, become three times their original size, forming a resisting membrane, which may almost be dissected; the villi are then pressed against each other, the epithelium forming four-fifths of their bulk. The epithelial cells also change in color, becoming whitish; this seems to be due to the large number of drops of fat found inside them, and the same phenomenon takes place even when the fluid of the stomach, which is brought in contact with the mucous, contains no fat. We know, however, that every cell contains fat; this fat, it is true, is disguised, but it becomes visible under certain circumstances, especially when an interior

* A, Intestinal villosity of man, taken from the jejunum. In *a* we see the columnar epithelium, with its nuclei, continuing as far as the surface of the villosity. *c*, Central chyliferous duct. *v*, *v*, Blood-vessels. The embryonic nuclei of the connective tissue are seen in the remaining part of the body of the villosity.

B, Villosity of a dog, contracted.

C, Villosity of man during intestinal absorption, the fat becoming a part of the body of the villus itself. In D a large collection of fat is seen. (280 diam.)

change takes place, which seems to be the signal of the death of the cell. It therefore appears probable, that the columnar epithelium, which we are considering, is near its end, that it will soon fall into decay, and that an *actual moulting* of the epithelium of the mucous will take place: this is what, we find, actually occurs. When the chyme contains fatty matters, this effect is still more apparent; the white is more brilliant and the fat globules larger: but here, too, the whole surface disappears, and a new epithelium takes its place.[1]

This whitish appearance and turgescence begin at the free base of the epithelium, extending gradually to its depth, and spreading over the whole villus (Fig. 69, C). It is always, however, the epithelium of the summit of this papilla which first becomes whitish and swollen, thus imparting to the villous projection a peculiar appearance, which enables us to understand what Lieberkühn saw, and explained by giving it the name of *ampulla* (small aspiratory reservoir of the chyle). The change in the mandrel of the villus follows that in the epithelium; and as the latter becomes granular, and is about to fall, the summit of the villus appears to change into a cluster of small drops of fat, which are seen first in the body, and then at the base of the villus, and are often more or less regularly ranged in rows. This would lead to the supposition that there are separate vessels, but it seems more probable that phenomena of nutrition are taking place in the plasmatic elements of the mucous, and that they are accompanied by metamorphoses similar to those which we have seen in the epithelium. These phenomena are still more striking when the intestinal fluid contains a large quantity of fat (Fig. 69, C, D).

This appearance is sometimes modified, especially in the dog (Fig. 69, B), by the deformation of the villus; but this is only an accessory phenomenon, and is caused by the contraction of the smooth muscular fibres. The body of the villus, in fact, contains rudimentary contractile elements, arranged, especially around the central chyliferous vessel, in striæ longitudinal to the axis of the villus; they are

[1] See Küss, "Gazette Médicale de Strasbourg." 1846, p. 38, *Sur l'absorption.*

Finck, "Sur la Physiologie de l'Epithélium Intestinal." Thèse de Strasbourg, 1854, No. 324.

L. Lereboullet, "De l'Epithélium Intestinal au point de vue de l'Absorption des Matières Grasses." Thèse de Strasbourg, 1866, No. 957.

curved in an arch, at the summit, and here Moldschott and Donders have discovered smooth contractile fibres (contractile cells) arranged transversely.

This is, in short, a phenomenon of passage: the epithelium, on account of its own life and its nutrition, becomes filled with the product of digestion with which it was in contact, and conveys this to the globular elements of the body of the villus which it penetrates; the phenomenon of diffusion is then all that is necessary in order that the blood may absorb the fluids which come in immediate contact with it. This phenomenon of passage has been examined chiefly in regard to the fats, because their optical properties render observation easier in their case, but the process is probably the same with the other elements (albuminoses and glucoses), though this cannot be directly ascertained: it is only by means of the fats that we can trace the process as it goes on.

Thus we see that in this phenomenon of *passage*, neither the phenomena of capillarity nor of *endosmosis*. are concerned; all this takes place in virtue of the special function of the epithelial cells, and of the plasmatic elements of the body of the villus; having arrived at this point the absorbed fluids only require to be diffused in order to spread throughout the organism, by means of organs which we shall study presently.[1] The passage of the sugars and the albumi-

[1] It is interesting to compare this statement, quoted word for word from Küss's lectures, with what Cl. Bernard has written in a recent publication: —

"Recent investigations, which are still unpublished, lead me to believe that digestive absorption is of an entirely different nature from all ordinary absorption. I have seen the pyloric glands of a frog disappear during winter, when digestion ceased, and reappear in the spring, when digestion recommences. Experiments which I have made seem to show that on the surface of the intestinal mucous membrane there takes place an actual generation of epithelial elements which attract the alimentary fluids, elaborate them, and then, by means of a kind of osmosis, pour them into the vessels. Digestion is not, therefore, simply a direct alimentary absorption. The aliments dissolved and decomposed by the digestive juices in the intestine simply form a generating blastema, in which the digestive epithelial elements find the materials of their composition and of their functional activity. In short, I do not believe in what may be called *direct digestion*. There is an organic or vital intermediate process. This is not simply a chemical solution, as most physiologists have imagined. I hope, in time, to be

noids could be explained, up to a certain point, by means of the physical theories of osmosis, but the passage of the fats was an insoluble problem, of which the only explanation that could be offered was that emulsion took place, or even decomposition or disengagement followed by reconstitution. We have seen that this is not the case, and that the fat is naturally absorbed. This view is confirmed by what so frequently takes place in other parts of the organism: the plasmatic cells of the deep layers of the dermis, and those of the mesentery, are quickly filled with a quantity of fat which they abstract from the blood, when the latter becomes saturated with it by means of abundant nourishment; this fat is sometimes very quickly appropriated, when the animal grows suddenly lean, as in the case of a cholera patient whose orbital fat disappears in a few hours. The fatty cells may then be observed to lose their fat, which is replaced by a serous fluid, which disappears in its turn, while the globule returns to its typical condition of a plasmatic globule; it cannot be urged that the influence of any special dissolving fluid is here exerted.

This fact can hardly be explained except by supposing that, in order to penetrate the economy, the fatty substances form, with the albuminoid substances, special combinations which may be compared with what we find in the medullary substance of the nerves; this instance of reabsorption may also be made use of in endeavoring to discover by what vascular organs the absorbed fat is carried off, whether by the blood vessels or the chyliferous vessels.

We have now to see what becomes of the epithelial cells which assist the passage, and what becomes of the substances which pass.

B. *Intestinal desquamation. Bile.*

After having conveyed the absorbed fluids (especially the fat, as may most readily be ascertained) to the tissue of the

able to show what conclusions we must draw from these new ideas on the subject." (Cl. Bernard, "De la Physiologie Générale." Notes, 1872, p. 283.) And farther on (p. 287), Cl. Bernard adds: "If the cells on the surface of the intestine be withdrawn during the work of digestion, atrophy speedily ensues. Thus I have found, on isolating a loop of the intestine in such a manner as to prevent the passage of the food, that atrophy of the mucous membrane soon followed, although the circulation went on as usual."

villus, the epithelium of the villus being now composed only of its albuminous elements, more or less liquefied, begins to fall into decay; fragments of it were long since found to exist in the intestine, but they were designated under the name of *crude chyle*. We find young cellular elements ready to take the place of this decayed epithelium.

It is at this instant only (7 or 8 hours after the ingestion of the food), that the bile is poured into the intestinal canal.

The *bile* is a fluid which it is difficult to study satisfactorily when it is contained in the biliary or gall-bladder of a corpse; because, under these conditions, it decomposes rapidly, especially when in contact with the mucus of this bladder; its color and its reaction are then changed. In order to form an exact idea of it, a fistula should be opened at the bottom of the gall bladder, through the coats of the abdomen, care being taken to tie the cystic duct (*ductus choledochus*), lest any fluid should escape into the intestinal canal. In this way, the bile may be collected, and the flow of the secretion will be found very abundant and almost uninterrupted, increasing in quantity, however, especially at a certain period of digestion. The quantity of water in this fluid has been estimated in the ratio of 20 to 1: the solid residuum is, therefore, 5 grammes to 100 grammes of bile. On the other hand, this solid residuum represents, for 24 hours, a mean weight of $\frac{1}{1000}$ part of the weight of the body: thus, in the case of man, whose mean weight is 65 kilogrammes, we find that, in 24 hours, the anhydrous bile would be represented by 65 grammes; on multiplying this figure by 20, we obtain 1 kilogramme, 300 grammes, as the weight of the bile secreted in 24 hours.

Under these circumstances it is also found that the natural color of the bile is not green, as it appears in autopsies (being impaired by the mucus of the vesicle) nor yellow, as is sometimes seen in vomited matter (being then changed by the action of the gastric juice). The natural color of the bile is green only in the case of the oviparous animals; in all the mammifera it is *yellow*, as may be seen in persons suffering from reabsorption of the bile, the yellowish tinge appearing in all the tissues, beginning with the white of the eye: the white of the eye of jaundiced persons is always yellow.

We ascertain, finally, that the normal bile is quite *neutral;* its mixture with the mucus sometimes imparts to it an

alkalinity which has led to the supposition that it has an important share in the process of digestion.

It may be said, briefly, to be composed of water, containing in solution three different elements: salts, cholesterine, and coloring matter.[1]

1. The *salts* of the bile are essentially what was formerly designated under the name of *biline:* this biline is now shown (Demarçais) to be a combination of soda with two fatty acids, cholic acid and choleic acid: these constitute the cholate and choleate of soda; these acids are also designated under the names of Taurocholic and Glycocholic (Taurocholate and Glycocholate of Soda) both being formed by the same acid, united in the one case, to glycochol, and, in the other, to taurine. In fishes these acids are combined, not with soda, but with potash.

It is generally admitted that the cholalic acid is originated in fatty substances; indeed, it is found strongly to resemble the oleic acid, for instance; it is not, therefore, a nitrogenous substance. *Glycochol* we know to be a nitrogenous substance, having a sweetish taste, and being derived from collagenous substances, whence the name of *sugar of gelatine. Taurine* is, also, a nitrogenous or azotic principle, but it also contains sulphur, and its decomposition in the intestine assists in producing sulphuretted hydrogen.

2. *Cholesterine* is a fatty substance which is not saponifiable; it is insoluble in water, but soluble in bile, on account of the choleate of soda existing in the latter; if the quantity of this salt is insufficient, the cholesterine is precipitated, forming those calculi so frequently found in the biliary reservoir. Researches by Flint seem to show that cholesterine is a waste produced by the life of the nervous elements (see p. 27).

3. The coloring matter is essentially represented by *bilifulvine*, a substance strongly resembling the blood pigment (hæmatoïn) from which it is derived; it is decomposed and precipitated very readily, yielding then various coloring matters, designated as bilirubine, biliverdine, etc.: green is the color most frequently found in decomposed bile.

[1] Table showing the chemical composition of the bile:—

Water		85	per cent.
Solid parts	Coloring matter, bilirubine	2	
	Biliary acids	8	
	Cholesterine	4	
	Salts	1	
		15	,,

This composition and the properties here enumerated supply us with very little information in regard to the probable functions of the bile in digestion. When the bile is turned out of its course by a fistula, and the animal is prevented from licking the wound, so that the bile can in no way enter the intestinal canal, the animal soon becomes emaciated: absorption takes place incompletely, especially that of the fatty substances which are found almost entire in the excrement, and the animal can only be kept alive by receiving twice or thrice its usual quantity of food. The pilous system of the animal also suffers greatly: the hair dries, becomes atrophied and falls; we shall see, however, that this is due to the fact that, in its natural condition, a large part of the bile is reabsorbed in the intestinal canal, and when it flows out of the body the organism suffers a great loss, especially in sulphur (taurine) since there are at least 3 grammes of sulphur in the bile formed during 24 hours; this sulphur forms an important part of all the elements of the epidermis, especially the horny productions (hair, nails, etc.).

In brief, the presence of the bile appears to be necessary to the accomplishment of the process of digestion and absorption. But how does it act? As we have foreshadowed, and upon which we must here insist, the bile is not poured into the intestine in such a manner as to come in contact with the product of the stomachal digestion; when the bile enters the duodenum, the contents of the intestine have already extended to the ileum, or even to the large intestine, and have been absorbed in a great measure. This fact alone, as well as the well-known properties of the normal bile (its neutrality, especially), renders it needless to attempt to disprove the numerous theories which have been suggested as to the action of the bile on the chyme.[1] Thus it was said that the bile being alkaline, and the chyme acid, these two fluids neutralized each other, and that, from the product of the stomach, the bile precipitated a crude chyme (*chyme brut*), under the form of flakes; these we have already shown to be simply produced from the epithelium by means of desquamation, which may, perhaps, take place under the influence of the bile. It was also supposed that this fluid finely divided or made an emulsion of the fats, etc.

Another class of theories, less opposed to facts than the

[1] See Blondlot, "Inutilité de la Bile dans la Digestion proprement dite." Nancy, 1851.

foregoing, but often quite as hypothetical, makes the bile to consist of a fluid which opposes the putrid fermentation of the contents of the intestine; indeed, when the bile is turned out of its course, and made to flow outwards, the fæces are found to acquire a very fetid odor. The bile is also sometimes supposed to be an excitant of the mucous and of the intestinal muscle; we have seen, however, that the erectile action of the villi belongs entirely to the epithelium, and takes place long before the arrival of the bile, under the exciting influence of the gastric juice alone: while, on the other hand, changing the natural course of the bile out of the intestine produces no effect on the motion of the muscular coats of this canal.

We take, finally, for our starting-point, the fact that the bile enters the intestine only when the process of absorption is nearly completed, and when the epithelium which has served for its passage, begins to decay and desquamate. The bile itself then appears to undergo several changes: its coloring matter is precipitated, and mixes with the fæces, imparting its own color to them; the case is the same in regard to the *cholesterine*, which is an excrementitial product; the remainder of the bile seems to disappear in the intestinal walls, and to become reabsorbed, not in its simple form, however, for none of its acids are found in the blood: it appears to be decomposed in the very act of penetrating the intestinal mucous coat.

This assemblage of facts, including the well-known one that the bile speedily dissolves all cellular elements (as may be easily observed in the blood globules), beside the circumstance that the greatest activity of the epithelial desquamation of the intestine takes place when it comes in contact with the bile; all justify us in concluding that the exudation and the action of the bile have some relation to this decay of the epitheliums. The chief purpose served by the bile is thus the renewal of the cellular coats, promoting the decay of the old elements, and the restoration of the new: if we may be allowed the expression, *it sweeps the workshop clean, in which the laborious task of absorption has just been completed*, and forms new epithelial organs ready to begin the process over again. This reconstitution takes place by means of the fresh cells which exist in the deeper portion of the epithelium. The intestine is, thus, never unprovided with epithelial cells: the new generation takes place so rapidly that it is impossible to distinguish it, half-hidden as it is by the ruins of former cells. We have seen that when

the bile is allowed to pass out of the body without going through the intestinal canal animals lose their power of absorption, especially of fatty substances: they continue in health, but require two or three times their usual quantity of food. Digestion, properly so-called, is not, therefore, impaired; it is only absorption, especially of fats, which is insufficient (since absorption is the process which requires the greatest activity on the part of the epithelium); the bile appears to be connected with the absorption of the fatty substances, by increasing the activity of the processes of renovation, desquamation, and vegetation of the epithelium.

C. *Functions of the Liver.*

The share taken by the bile in intestinal functions, especially in absorption, has already shown us the physiological importance of that large viscus called the liver; we have seen that this organ has some effect upon the composition of the blood, the formation and destruction of its globular elements, particularly the red globules (see *blood*, p. 124). Cl. Bernard's researches have finally revealed new functions in this organ, *glycogeny*, showing it to have at least as much effect on the constitution of the serum as on that of the morphological or physical elements of the blood.

We have already said (p. 233) that the liver is formed of two glands, each of which penetrates the other; namely the biliary gland and the vascular blood gland (Fig. 70). We have studied the functions of the biliary gland; which are quite independent of those of the vascular gland, especially from the stand-point of glycogeny (Cl. Bernard); study of the development of the liver from the embryo serves to exhibit this independence, especially in an anatomical point of view (C. Morel. See p. 232.) Numerous and, perhaps, still more interesting proofs of it are to be found in the facts borrowed from pathology.

Thus, in cirrhosis of the liver, an affection of the connective tissue of this organ, although the great hepatic cells (glycogenic liver), are impaired by compression, or even destroyed, the secretion of the bile, and, later, its pathological reabsorption (jaundice) goes on as usual, the canaliculi, or secreting tubes, of the bile not having been first attacked.

The *fatty degeneration* of the liver, which affects only the larger cells, produces no change in the secretion of the bile; and in very large livers whose substance has been changed almost entirely into fat, a considerable quantity of bile is still

found in the gall-bladder and in the tubes, the biliary liver remaining comparatively uninjured. If the larger cells were the secreting element of the bile, it would be impossible to

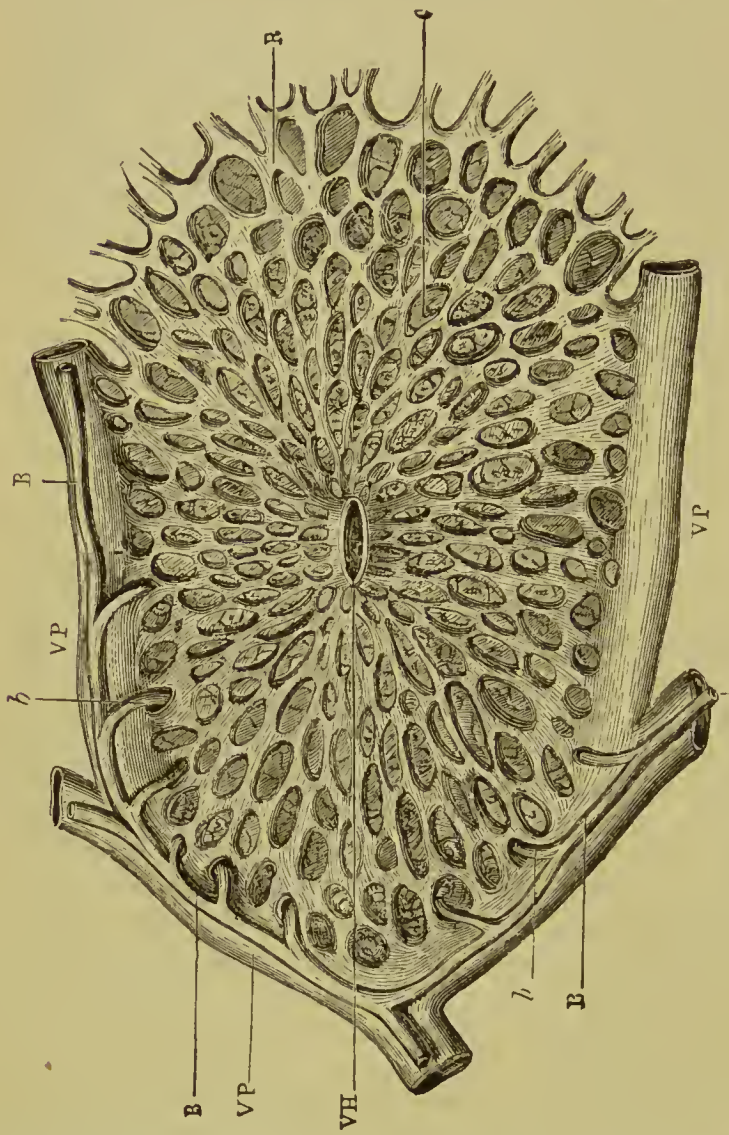


Fig. 70. — Hepatic lobule, showing the liver to be a double gland *

* VH, Hepatic vein, which takes its rise in the centre of the hepatic lobule. VP, VP, VP, Termination of the *vena porta* around the hepatic lobule: from these divisions of the *portal vein* proceeds a system of intermediary capillary vessels between the portal vein and the hepatic vein. In the meshes of this capillary network are situated the hepatic cells G, which are in close contact with the blood of the portal vein. B, B, B, Termination of the biliary ducts, or rather origin of these tubes around the hepatic lobules. (Cl. Bernard.)

comprehend how secretion could continue; these cells when thus completely infiltrated with fat, from a physiological point of view, are only defunct globules.[1] Numerous and recent histological researches, however, having for their object the

[1] See P. A. Accolas, "Essai sur l'Origine des Canalicules Hépatiques, et sur l'Indépendance des Appareils Biliaire et Glycogène du Foie." Thèse de Strasbourg, 1867, No. 19.

origin of the hepatic canaliculi, seem to show a connection between the large hepatic cells and the biliary organs, which is, perhaps, closer than that indicated by Küss, Morel, Handfield Jones, and Ch. Robin (Dict. de Nysten). The agreement of the results obtained by numerous histologists, in France (Robin, Legros, Cornil), as well as in other countries (Gerlach, Andréjevié, MacGillavry, Chronszewsky, Hering, Eberth, etc.), obliges us to consider these researches of importance, and we shall find that physiological data correspond with these results.[1]

Lereboullet was,[2] 1853, convinced by his experiments on the fatty liver, that the origins of the biliary tubes are simply empty spaces which are arranged in series (intercellular *meati*), hollowed out between the cells: these empty spaces are entirely accidental, and would be produced in anatomical preparations by the passage of the injected matters.

These spaces have been the subject of much investigation: they are known by the name of *biliary capillaries*, or *intralobular canaliculi.* Kölliker, as well as the other histologists whom we have mentioned, has succeeded in distinguishing them, and considers them to be simply *intercellular lacunæ* having no proper coats, or being covered only with a sort of *cuticle* which Kölliker looks upon as belonging to the cells between which the lacuna is situated: "I should prefer to consider this cuticle as a cellular membrane, and to say that it is more developed in the region of the biliary capillaries than in any other part." (French trans. 1870, p. 568.)

According to some anatomists (MacGillavry, Frey), these canaliculi are furnished with a coat of their own, the large hepatic cells being situated outside; Legros' researches show that this coat is lined with a pavement epithelium. We are finally brought back to the idea of a biliary gland, which is quite distinct from the vascular blood gland, although the mutual association between these two organs appears much closer than the researches made five or six years ago would lead us to suppose. "In the interlobular ducts the epithelium is more distinctly columnar than in the branches of the hepatic duct properly so called: but in the *intralobular canaliculi*, it is a true pavement of small cells, which, by their proximity to the secretory canaliculi, form the coats

[1] Lereboullet, "Mémoire sur la Structure intime du Foie et sur la Nature de l'Altération connue sous le Nom de Foie Gras." Paris, 1853, in 4to.

of these vessels; *these cells thus form an organ quite distinct from the much larger one constituted by the hepatic cells, properly so called* (Ch. Robin, "Du Microscope," 1871).

The final results obtained by histology are not thus opposed to the physiological distinction made between a biliary and a glycogenic gland. It appears, however, that the great question of the physiology of the liver is not yet solved; for recent physiological and experimental researches seem to show that the glycogenic function is by no means peculiar to this organ, as was at first so firmly believed, but is a property common to all the tissues, and only carried to a slightly higher degree in the hepatic organ. These researches are chiefly connected with the study of *diabetes*, and, with regard to this disease, we shall see that it is going too far to completely deny the glycogenic functions of the liver (Vulpian, Cours de mai, 1872).

Cl. Bernard first proved that animal as well as vegetable organisms produce sugar. Magendie had, before this, discovered sugar in the blood, but in the herbivorous animals only; Cl. Bernard proved that it also exists in the carnivora, but that scarcely any signs of it are found in the portal vein, while a comparatively large quantity is found in the hepatic veins. He also showed that the presence of this sugar cannot be accounted for by any such storing up of the saccharine elements of the food received as occurs in the case of certain poisons, but that sugar exists in the liver quite independently of external supply. The sugar produced in the liver he shows is similar to that found in the urine of patients suffering from diabetes, and that this disease is only a pathological exaggeration of the normal glycogenic function. This function of the liver begins in the fœtus, apparently only at the age of three or four months: before this time, the placenta seems to perform a similar office, by means of a layer of glycogenic cells, placed between the fœtal and maternal placenta (Cl. Bernard, 1847–1855).

Cl. Bernard soon became convinced that the globular elements of the liver do not form sugar directly, but rather that there is a substance which is capable of being transformed into sugar, a *glycogenous substance* resembling starch, and which is changed into glucose by means of the same agents as starch. This glycogenous substance can only be changed into sugar in the organism by the action of a ferment which is produced in the liver, or brought into it by the blood. Bernard became convinced of this by observing that the

quantity of sugar in the liver varies according to the circumstances under which it is examined; if, immediately after the death of the animal, it is always found to contain less sugar than on the following day; this is because the glycogenous matter is changed into sugar after death (Cl. Bernard, 1855, 1859). Schiff, on meeting with this glycogenous matter, gave it the name of *inuline*, wrongly supposing it to resemble a vegetable starch, although it has neither the same microscopical features nor the same reactions. Rouget gave this substance the name of *zoamyline* (or animal starch).

Cl. Bernard then attached great importance to the glycogenic function of the liver, and he considered sugar as an essential element in the composition of those fluids in which cells are developed: he believed that he saw cases of spontaneous generation in saccharine fluids; he looked upon sugar as the most indispensable principle of the life of the organic elements; he even went so far as to attribute the almost certain death of those animals, whose two pneumogastric nerves have been cut, to the fact that by this means the glycogenic functions of the liver are arrested.

These exaggerations produced a strong reaction, and the attacks made upon the theory of glycogeny brought about the discovery of some important facts. The theory was defended by Cl. Bernard, Lehmann, and Poggiale, and disputed principally by Figuier, Colin, Chauveau, and Sanson. Sanson proved that meat, muscular flesh, contains a saccharine substance, and that an extraordinary quantity of this substance is produced in the animals experimented upon, by feeding them with butcher's meat; this muscular sugar is, however, dextrine and has no connection with the glycogenous substance of the liver. Rouget showed that this glycogenous matter, or *zoamyline*, is not at all peculiar to the hepatic tissue; that it represents a collateral product of the nutrition of all the tissues, and is chiefly found in large quantities in the fœtus and in young subjects: first, in the bone-cartilages of the members; then in the muscles (the muscular plasma only); then in all the epitheliums, from the epithelium of the placenta, between the fœtal and the maternal organism, to the epidermis, the pulmonary vesicles, and the glands of Lieberkühn, and, finally, to the epithelium of the vagina, where it is found even in the adult female. He considers glycogeny as a general feature of the life of the tissues, and its exaggeration as an accidental circumstance in the nutrition of the liver.

With regard to diabetes, the disease which first gave rise to the whole question, and to which it must always be referred in physiological investigations, as well as in pathogenic researches, it must be admitted that the liver is the chief actor, without, however, attributing to hepatic glycogeny the important physiological function at first ascribed to it by Cl. Bernard.

Does the glycogenous substance, however, which in pathological cases is undoubtedly changed into sugar, constantly undergo in a more or less decided degree the same transformation when in the physiological state? When the animal is living and in perfect health, does the liver elaborate sugar incessantly? Here this vexed question of glycogeny rests for the present. Cl. Bernard has no hesitation in supposing this incessant physiological transformation. In this opinion he is opposed by Schiff and Pavy. These two experimenters maintain that the sugar found in the liver is always formed *after death:* in a fresh liver, taken from an animal just killed (Pavy, Schiff, Ritter),[1] or, better still, from a living animal (Meisner, Jäger), no sugar will be found, but only glycogenous matter which is not transformed into sugar in the living animal, either for want of a ferment which is capable of producing this transformation (Schiff), or because this ferment, though existing, cannot act during the life of the animal on account of certain influences arising in the nervous system which are opposed to it (Pavy).

This view is, evidently, an exaggerated one. These experiments merely show that in the normal condition the transformation into sugar is very trifling, and not easily exhibited by means of the reagents which we possess. An American physiologist, however, Dalton, experimenting with a care and rapidity at least equal to that displayed by Pavy, has succeeded in demonstrating that the living liver is not entirely without sugar.

The liver thus forms glycogenous matter: this matter is changed into sugar by the action of a ferment the origin of which is as yet undecided.[2]

[1] See Schiff, "Nouvelles Recherches sur la Glycogénie Animale." (In Journ. de l'Anat. et de la Physiol., de Ch. Robin, 1866, Nos. de juillet et août.)

[2] Claude Bernard's researches on the subject of glycogeny may be summed up in the following manner: "In 1848 he discovered sugar in the liver; it is always found there, whatever may be the nutrition of the animal. In 1855 he demonstrates that the sugar

The sugar thus formed is poured into the blood, and, being drawn on by the current of the circulation, soon disappears, being either consumed in the lungs or destroyed by oxidation, or by some other means in some part of the economy. In this way little or no sugar is left in the blood, but whenever the quantity formed is too considerable, and is not completely destroyed, glycæmia ensues; and if the quantity exceed three per cent of the solid residuum of the blood, or if it is more than from two to three grammes to every kilogramme of the animal's weight (Kühne), the sugar is excreted by the kidneys, and the glycæmia appears as glycosuria or *diabetes*.

This increase in the production of sugar, and the consequences which follow, may be artificially produced by various methods, which confirm the theory of hepatic glycogeny, by more or less directly affecting the liver.

Thus the injection of irritants into the portal vein (ether, Harley) brings on glycosuria. This is, no doubt, the effect of certain more or less poisonous substances when absorbed by different organs, such as chloroform, woorara (?), putrid matters, etc.: the latter, no doubt, help to increase the ferment necessary to change the glycogen into sugar. All those conditions, in fact, which are favorable for fermentations serve to produce and increase diabetes, while all those which hinder fermentation tend to diminish or even to check it

of the liver is derived from a substance formed in the liver, which substance he examines (1857), finding in it features resembling those of vegetable starch. In 1859, while seeking for the origin of this *glycogenous substance*, he found it to exist in the placental organs of the mammalia, in the vitelline membrane of birds, and in the inferior animals when in the larval or chrysalid state. He then shows that the glycogenic cells are first found on the inner surface of the amnion of the mammalia, where, about the middle of gestation, they form well developed papillæ, disappearing afterwards when the glycogenic function becomes established in the liver. In birds the glycogenic cells are first placed along the passage of the omphalo-mesenteric veins, and then at the extremities of the vitelline veins, which form actual glycogenic villi floating in the substance of the yolk. The glycogenic substance is thus at first diffused throughout the organs of the embryo in a transitory form, and only finally appears in the liver, where it remains. On the other hand, animal glycogeny really constitutes a chemical evolution of the starchy elements, an evolution which resembles, or, rather, is identical with that exhibited by the starch found in vegetable organisms (Cl. Bernard, Cours de 1872).

entirely. Thus Wingradoff has shown that frogs, in which this disease has been produced, recover if put in a cold place, a low temperature serving to check fermentation; but the disease reappears if the animal be replaced in an atmosphere sufficiently warm to allow of fermentation taking place.[1]

The most remarkable case, however, of diabetes artificially produced is that in which it is caused by special modifications wrought in the nervous system. Cl. Bernard discovered that if a puncture be made in the floor (in P′, Fig. 71) of the fourth ventricle of an animal (a rabbit), between the roots of the auditory and those of the pneumogastric nerves, sugar is found a short time afterwards (an hour and sometimes less) in the urine of the animal. (A puncture made a little higher up, as at P, produces glycosuria, accompanied by polyuria; a little higher up, the puncture produces albuminuria.) This glycosuria is caused by the hepatic function, Wingradoff having shown that if the fourth ventricle of a frog be pricked, thus producing diabetes, the disease will disappear if the liver, which is the sugar-producing organ, be removed. We know, on the other hand, that after a long course of slow poisoning by arsenic the liver loses its glycogenous matter and thus the power of producing sugar; and, in this case, a puncture in the fourth ventricle of an animal does not produce diabetes.

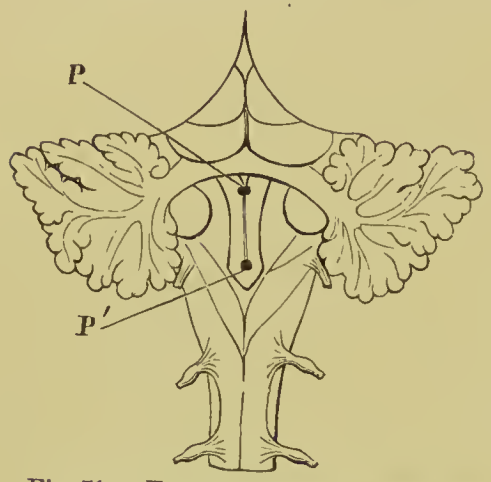


Fig. 71. — Fourth ventricle (rabbit) and experimental punctures.*

The nerve-tract which unites the fourth ventricle to the liver appears to belong, not to the pneumogastric, but to the great sympathetic nerve, as was imagined by Cl. Bernard, and directly proved by Schiff and Moos: the latter, espe-

[1] See Cl. Bernard, "Cours du Collége de France." (In Revue des Cours Scientifiques, avril, 1873.)

* The lobes of the cerebellum are separated: below are seen the restiform bodies whose divergence surrounds the point of the calamus scriptorius and the fourth ventricle. The puncture P′, which produces *glycosuria*, is situated a little above the point of the calamus. The puncture P is made at the level of the tubercles of Wenzel; that is to say, the origin of the auditory nerves. (Cl. Bernard.)

cially, has shown that, if all the sympathetic nerves leading to the liver of a frog be tied, diabetes can no longer be produced, either by puncture of the fourth ventricle or by electrical excitation of the spinal cord. In all these cases violent hyperæmia of the liver appears to be necessary to the excitement of its glycogenic functions; indeed, if the inferior vena cava below the liver in a frog be tied, an increase of circulation in the portal vein is produced, followed by diabetes. This increase of circulation is caused by the anastomoses existing in this animal, between the venous system in general and the system of the portal vein. The congestion of the liver and excitation of its glycogenic function which follow a puncture made in the fourth ventricle do not, however, appear to be produced simply by a (nervous) paralytic hyperæmia, arising from the abolition of the vasomotor innervation; because the artificial diabetes thus produced is but temporary (lasting, at the most, twenty-four hours). This diabetes appears rather to arise from the *excitation* of certain nerves included in the network of the great sympathetic nerve, and which are to the liver what the chorda tympani is to the sub-maxillary gland (Cl. Bernard).

D. *Organs of absorption. — Function of the chyliferous vessels.*

We have seen how the digested matters reach the very substance of the villus by means of the epithelium. While the epithelium is being renewed (desquamation, etc.), the body of the villus empties its contents, and the absorbed elements are diffused into or through the vessels.

These vessels, however, are of two kinds: we have seen that there is a vascular blood network, forming the origin of the portal vein, and a central chyliferous vessel, the origin of the chyliferous vessels, which open into the principal trunk of the lymphatic circulation (thoracic duct. See *lymphatic system*, p. 156). The blood current, being placed so near the surface, is evidently in the most favorable situation to absorb whatever is brought to it by the epithelium: it is, therefore, generally supposed that the greater part of the absorbed matters are carried along by the blood; and it is true that we find the peptones and glucose again in the portal vein. But, while the fat is disappearing from the villus, we find that the central chyliferous vessel becomes quite white, and that a large number of delicately emulsionized fat molecules make their appearance in it; this seems to show that

the fats do not pass through the same organs as the preceding substances, and that the chyliferous vessel is especially appointed for their absorption.

We may, indeed, suppose that the fat contained in the intestine, is absorbed by the cells of the villus (epithelial and plasmatic cells), and that it is excreted by them into the central chyliferous vessel. We have already considered the lymphatic vessels as appointed to collect the deeper residuum, the waste produced by the life of the epitheliums (see p. 194).

The fat does not, however, pass through the lymphatic organs only; it is also found in the blood, although the quantity there is very small. The other matters which have been absorbed are also met with in the chyliferous vessels, but their quantity, compared with that of the fat, is infinitesimally small.

Some authors, however, entirely deny that the vessels of the portal circulation have the power of absorbing and carrying off the fat.[1] This is because the fat found in the blood is not in the same state as in the chyle: in mammal's blood the fat is never in a free state, but always saponified; it is, no doubt, saponified by the choleate of soda in the bile.

Most poisonous substances are absorbed by the veins; intoxication taking place so rapidly that the poisons can scarcely be supposed to pass through the lymphatic organs.

Metals absorbed in the form of metallic salts, accumulate in the liver. This is an important fact, for it shows that the liver retains a large proportion of the alimentary substances for the purpose of modifying them. The albumen is transformed, because it comes in contact with the hepatic cells by means of the portal circulation.

We find, in short, that our knowledge of this interior process of absorption is still very incomplete. We have been occupied in studying these phenomena in reference to the *living cells* in which absorption takes place, and we have considered the process of absorption as an essential feature of these globules. We have, therefore, paid little attention to the physical theories of absorption, or to experiments made with membranes deprived of life. Experiments of this kind have led to the belief that absorption is simply a phenomenon of osmosis. Thus J. Béclard considers the current of absorp-

[1] See Béclard, "Recherches Expérimentales sur les Fonctions de la Veine Porte." (Arch. Génér. de Médecine, 1848.)

tion as produced by the difference in the specific heat of those fluids which surround the membrane to be traversed: he looks upon the osmosis which then takes place as a physico-chemical property, in virtue of which the miscible fluids have a tendency to mix in the membrane, one current predominating over another. All other things being equal, the direction and intensity of the current are determined by the differences in specific heat. The figures given by J. Béclard, in support of this theory, showing the specific heat of the different fluids, agree perfectly with what we know of their flowing towards each other. However plausible this theory may appear, it is only a physical theory of *osmosis;* and knowing, as we do, the important function of the living cell, we cannot imagine that, in the phenomenon of *intestinal absorption*, it simply plays the part of an inert membrane.

V. Large Intestine.

The aliments that pass out from the stomach form a fluid mass; we have seen that they become still more fluid by the addition of the pancreatic and enteric juices. However, as these matters pass through the small intestine, their consistency increases, while their bulk diminishes, the greater part being absorbed. The small intestine, therefore, delivers to the large intestine only a solid substance, or waste, which is to be thrown off, and is prevented from passing back again by the *ileo-cæcal valve*, which renders any reflux impossible. In man, very little digestive action takes place in the large intestine; the small amount which has escaped absorption are here, however, drawn into the blood current, and the large intestine may even absorb fluids directly introduced into it. After injection, by the rectum, of fatty substances (fats in a state of emulsion), the lymphatic vessels leading from the large intestine exhibit the same features, the same chyliferous appearance, as those of the small intestine. The villi are not found here, but their place is supplied by numerous folds in the mucous membrane. In herbivorous animals, whose cæcum is very much developed, this part of the intestinal tube is the seat of actual digestive phenomena: the cœcum may therefore be considered as a sort of second stomach; it contains acids which suffice for the digestion of the vegetable albuminoids. It is not certain that these acids are secreted from its walls: they are, more probably, produced by the aliments themselves. They increase in

quantity with the increase of substance in the canal. These acids are generally the lactic and butyric acids, arising from the fermentation and decomposition of the sugars and the fats.

Half-way through the large intestine, however, all digestion and absorption cease: the tube contains only those matters which are to be thrown off, — the *fæces*, in short. The fæces have been wrongly considered as principally formed of that part of the food which cannot be assimilated: if this were true, if all the nourishment received can be absorbed, there ought to be no fæces, and yet they appear, even in this case. Thus the fœtus, whose digestive tube is as yet empty, immediately after birth expels fæces which are well known under the name of *meconium:* the meconium is formed of remains of epithelial cells, colored yellow by the bile, which, not having yet become decomposed, preserves its natural color. This explains why the principal product thrown off, and of which the fæces are chiefly composed, consists of *remains of the desquamated epithelium:* sometimes, even in the adult, these remains alone form the substance of the fæces. They appear either as entire or as mutilated globules of a whitish color, variously tinged by the decomposed bile. These epithelial remains somewhat resemble the fine scales which fall from the cutaneous epidermis, but they are more numerous and important than this; for we have seen that the shedding of the epithelium is the fatal termination of the series of phenomena of absorption, and that the principal use of the bile is to regulate and to hasten its production.

Those parts of the aliments and of the digestive fluids which cannot be assimilated can only be classed as secondary elements in the constitution of the fæces. Among these are cholesterine and the coloring matter of the bile which are precipitated when this fluid enters the intestine; also fatty substances, when ingested in too large quantities; amylaceous substances protected by too thick a covering of cellulose; and cellulose, in general, with its derivatives. Indeed vegetable aliments contain the largest quantity of substances which resist digestion, and the fæces of the herbivorous animals are, therefore, much more abundant than those of the carnivora. Animal food, however, also contains elements which long resist the influence of the digestive juices: thus the horny growths of the epidermis (hair, nails, etc.), and the yellow or elastic tissues (parts of tendons, of arterial coats, etc.), are found in the fæces almost entire.

These substances are carried, by slow, peristaltic contractions, into the sigmoid flexure. Here they apparently pause, and are carried into the rectum, in an intermittent manner only, under the influence of stronger contractions; they here tend to produce the reflex phenomenon which we shall study under the name of *defecation:* if this attempt at evacuation, however, does not succeed, and the passage is closed to them the fæces return to the sigmoid flexure. These movements are all extremely slow and of such a character as to produce considerable compression throughout the length of the lower end of the gut. As in the case of the small intestine, the form and mode of production of these movements are not yet perfectly known; they are *peristaltic* movements, that is, movements in which the circular fibres of the muscular membrane contract, proceeding in a downward direction, causing the substances to pass through the intestinal tube; thus any substance being compressed above, is forced into the lower part of the intestine, the fibres of which are still relaxed. Those movements called *anti-peristaltic*, which take place in the contrary direction, and thus have the effect of forcing back the contents of the intestine, do not appear to exist in the living animal, when in its normal condition.[1] They are evidently produced in certain pathological cases. Those, observed in the intestinal canal of an animal in which the abdomen is opened immediately after it has been killed, appear to be owing to an interruption in the abdominal circulation, causing ultimate excitation of the smooth fibres, at the instant of death. We have scarcely any means of deciding on the nature of the reflex mechanism by which the nervous system influences or produces these movements. The *solar plexus* may, perhaps, serve as the centre of these reflexes; embryology, indeed, shows that this abdominal nerve centre appears to be developed independently of the spinal cord. The solar plexus is, however, united to the cord by two large nerve commissures, if they may be so called, the pneumo-gastric and the splanchnic nerves; it is remarkable that excitation of the former produces or increases the movements in the intestines, while excitation of the latter (great splanchnic nerves) appears to render the viscera motionless, and paralyzes their muscular

[1] See Braam-Honckgeest, "Untersuchungen über Peristaltik des Magens und Darmkanals." (Pflüger's Archiv., September, 1872.)

walls. The splanchnic nerves are, therefore, to the intestines what the pneumo-gastric nerve is to the heart, that is an *arresting nerve* (Experiments by Pflüger).

Onimus and Legros studied the movements of the different parts of the digestive canal by means of a registering apparatus, upon which a lever (set in motion by an india-rubber bag introduced into the intestinal tube, and which set in action its contractions) recorded these contractions as they occurred. While engaged in this study, they observed that, by galvanizing the pneumo-gastric nerve by means of interrupted currents, the movements of the intestine may be checked, and *checked, not when in a state of contraction, but when entirely relaxed.* "In this case a very remarkable depression is obtained in the tracing, and it is important to associate the fact of the checking of the heart in *diastole*, and the checking of the respiratory movements in *inspiration*, during the excitation of the pneumo-gastric nerve by interrupted currents" (see p. 40).

It is easier to explain what goes on at the lower extremity of the digestive canal, this part being more accessible, and the phenomenon of *defecation* thus becoming perfectly plain. First, it must be recollected that the longitudinal muscular fibres form in the rectum an extremely thick and powerful stratum, and that, on the other hand, the circular fibres are grouped together and multiplied in such a manner as to form a sphincter or ring, called an *internal sphincter*, formed of smooth muscular fibres, and enclosed in another and more powerful sphincter, called the *external sphincter*, which is formed of striated fibres. These sphincters do not exactly form a ring, but rather an *antero-posterior button-hole*, confined by two muscular bands, which, during the state of repose, are quite close together. When in repose, this sphincter, by virtue of its elasticity alone, completely closes the opening which it surrounds, as is the case indeed with all the sphincters (see *Physiology of the muscle*, natural form of the muscle and sphincters when in the state of repose, p. 72). These contractions, therefore, are no more permanent here than elsewhere: the ring-like aperture is normally obliterated by the natural form of the sphincter, and the sphincter contracts only when some body seeks to modify its form, in order to dilate the orifice which it surrounds. Under these circumstances either the sphincter does not react, but dilates readily, on account of its great elasticity, and the passage takes place; or else the sphincter reacts, and by its contrac-

tion closes the orifice in a really active manner: in the former of these two cases *defecation* is produced.

Defecation is a reflex phenomenon of expulsion, the centre of which is found in the lower part of the cord, as is proved by pathological cases. At the beginning of this reflex, a vague sensation is experienced, which can hardly be defined, a feeling of weight in the perineum produced by the presence of the fæcal matter. The seat of this sensation, the *desire*, is in the rectum only; in the other parts of the large intestine these substances are not normally felt. In cases of artificial anus, however, following strangulated hernia, and having their seat in any part of the intestinal tube, it has been remarked that as the alvine matters approach the artificial orifice a vague sensation is felt, resembling that of the necessary promptings of nature; which seems to prove that this sensation may be experienced in any part of the intestinal tube, it being, perhaps, only due to the weight and pressure of the fæcal substances brought together in a mass (Bert).[1]

Under the influence of this feeling a series of expulsive efforts are made, which are reflex, as we have said, but are under the influence of the will, either by increasing their force or checking them. If the desire is not satisfied, an anti-peristaltic movement takes place, beginning at the anal sphincter, which drives the excrement back into the sigmoid flexure, whence, after a time, they return to try the passage again. If this attempt be resisted several times in succession, the rectum at length loses its sensibility, and the presence of the excrement ceases to give rise to the reflex action which we are about to study; this is the cause of the habitual constipation of persons who neglect the signs mentioned, and who soon find themselves obliged by artificial means (suppositories) to excite the dulled sensibility of the mucous membrane of the rectum and of the nervous fibres which govern the centripetal part of the reflex.

If attention is paid to the promptings of this desire, a reflex contraction of the muscular walls of the rectum takes place naturally; this is a genuine peristaltic movement, by means of which the excrement is discharged into the anus, the sphincter of which, dilating readily, offers no resistance. If the fæces, indeed, are in an abnormally fluid state, the

[1] See Paul Bert, Art. *Défécation*, du "Nouveau Dict. de Médecine et de Chirurgie Pratiques." Vol. X., p. 747.

rectum alone can expel them, without the will having any other share in the matter than that of not offering any obstacle to their passage. In ordinary cases, however, the solid state of the excrement requires the intervention of more numerous and considerable forces, which act principally under the influence of the will: the first is the phenomenon of *straining*, by means of which the larynx closes, causing the walls of the thoracic cavity, which is filled with air, to supply a fulcrum to the muscles which are about to act; all those muscles which can compress the abdomen, that is, the muscles of the abdominal coat, the diaphragm, and the muscles of the perineum (*levator ani*), then contract, producing compression on every side. The levator ani, while compressing the viscera from bottom to top, brings just in front of the excrement the orifice through which it must pass. The longitudinal fibres of the rectum, which are so largely developed, act for the same purpose, and this is only one mode of the mechanism which we studied when analyzing the peristaltic movement (see *Deglutition*, p. 225). Moreover, these longitudinal fibres terminate below by folds, which disappear more or less distinctly in the perineum, forming a convex curve directed towards the centre of the anus; whence it follows that during their contraction their curve straightens, and, consequently, dilates the orifice through which the excrement is to pass.

PART SEVENTH.

PULMONARY MUCOUS TISSUE. — RESPIRATION. — ANIMAL HEAT.

I. RESPIRATION.

The surface of the respiratory mucous[1] is that which, next to the epithelial surface of the digestive tract, most readily yields to interchanges of nutrition; these interchanges are, however, in the normal condition, chiefly gaseous. As the absorption of the substances, called alimentary, occurs slightly over all the surfaces, and as we have seen that the reabsorption of fat happens in all the tissues, — although these phenomena have their *special* seat at the level of the epithelium of the digestive tract, — so the gaseous interchanges take place over many surfaces, for instance, in ths skin, and the gases may be reabsorbed in the most interior portion of the tissues (as in sub-cutaneous emphysema); yet these phenomena are connected chiefly, in the superior animals, with the *respiratory mucous*.



Fig. 72. — Ramification of the pulmonary pouch in the fœtus of a sheep, length one inch and a half (Müller).

The *respiratory mucous* may, from an embryological point of view, be considered as an offshoot of the sub-diaphragmatic part of the digestive tract; indeed, the first appearance of the lungs in the fœtus exhibits the form of a growth of the epithelium of the anterior wall of the pharynx. This

[1] It may have been noticed that the word "mucous" has been used frequently as referring to the mucous coat, tissue, or membrane.

offshoot, which is at first solid, becomes hollow and bifurcated as it is developed (Fig. 72): the epithelium at the same time undergoes a change; from having been pavement in the pharynx it becomes columnar and vibratile in the pedicles of the offshoots (*trachea and bronchi*), and pavement again in the air sacs or pouches (*alveoli*). The lungs may thus be compared to a gland, the pouches of which are

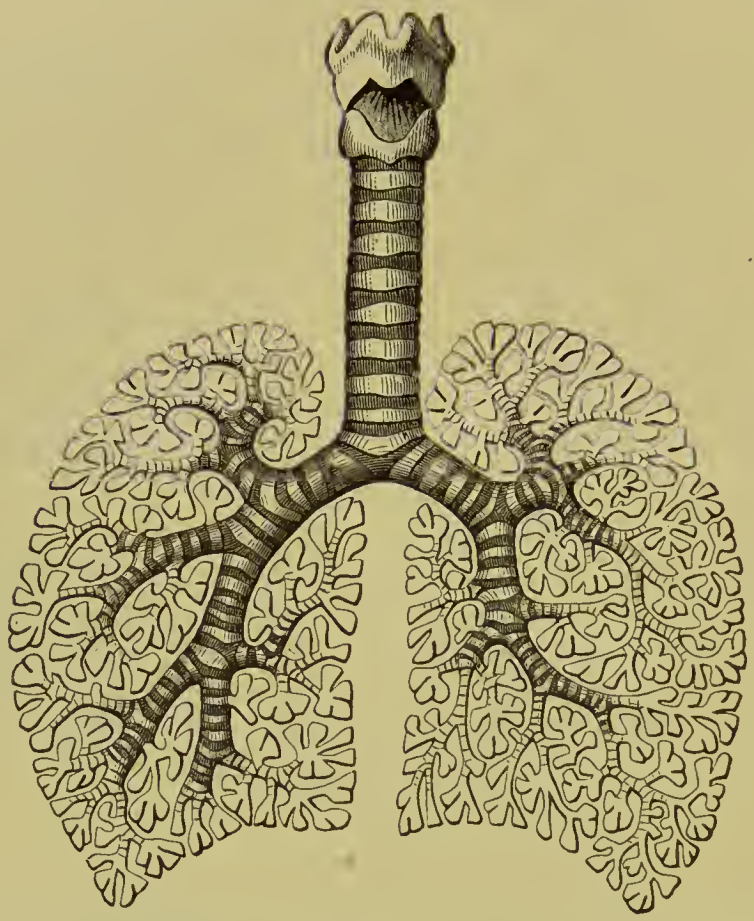


Fig. 73. — Larynx of a man, trachea, bronchi, and lungs, with the ramification of the bronchi and the division of the lungs into lobules. (Dalton, "Human Physiology.")

represented by the *alveoli* (Fig. 73), and the excretory tubes by the *bronchi*. These pouches may be likened to a conical and pyriform but indented organ, the summit of which is prolonged by a bronchial ramification: this *ampulla* (Fig. 74), which is about one-eighth of a millimetre in diameter, has not a simple form, but is uniformly embossed on the inside, where it presents a number of prominent folds, dividing the primitive alveolus into a great number of secondary alveoli

or *vesicles* (Fig. 74, *c*, *c*). The alveoli join together, forming *lobules*, which are easily distinguished on the surface of the lung in a system of network (division lines of the lobules), and the lobules themselves, uniting, form the *lobes of the*

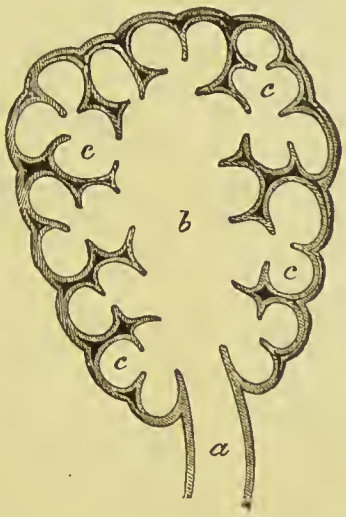


Fig. 74. — Lobule of the lung in man.*

lung. The alveoli are, therefore, very numerous; their number has been estimated approximately as seventeen or eighteen hundred millions.

I. Structure of the Respiratory Membrane. — Arrangement of its Parts.

The pulmonary alveolus constitutes essentially the respiratory surface: it consists of epithelium and a substratum of connective tissue.

1. The pulmonary epithelium is formed of epithelial layers, extremely delicate and not readily observed, arranged in a single row, and frequently at a considerable distance from each other.[1] In the normal state its elements exhibit very

[1] See Ch. Schmidt, "De l'Épithélium Pulmonaire." Thèse de Strasbourg, 1866, No. 931.

The existence of the pulmonary epithelium was, for a long time, disputed. Villemin was one of its most ardent opponents, which is not to be wondered at when we consider the elaborate process of

* *a*, Termination of the bronchial tube. *b*, Cavity of the lobule. *c*, *c*, *c*, *c*, Air-cells or vesicles. (Dalton, "Human Physiology.") This *sac* or pouch exactly represents the whole lung of a frog.

few metamorphoses and scarcely any epithelial *remains:* they even show a tendency to waste away with age; and the walls which supported them also falling away, what is called

preparation which he thought neeessary for the study of the pulmonary lobules (desieeation, biehloride of mereury, water of ammonia, and, finally, iodine. Now the pulmonary epithelium is the most delieate of all the tissues, and requires the same proeess of preparation as the most delieate epitheliums of the serous tissue. Elenz (in 1864), by means of nitrate of silver, aseertained the existence of a pulmonary epithelium in all the vertebrated animals, and his observations have been since confirmed by others. Sehmidt (*op. cit.*), by employing the same method, arrived at the following

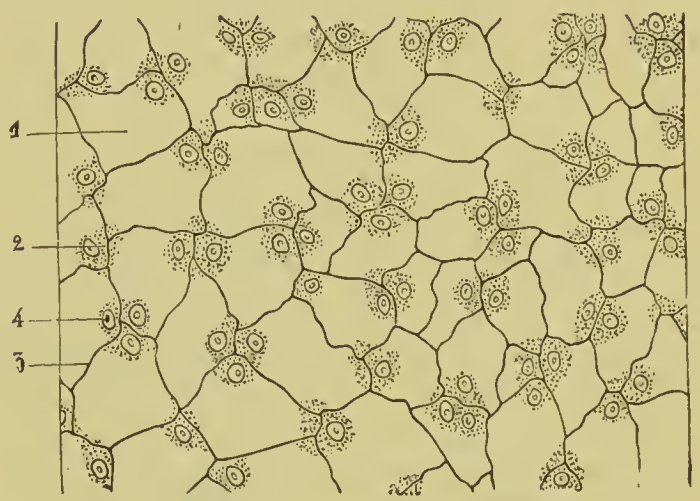


Fig. 75. — Pulmonary epithelium.*

conclusions: in the mammalia the pulmonary vesieles of the embryo are lined with regular eells, all of uniform size; in the newborn animals some of these eells beeome larger and eover the eapillaries, while the rest remain unehanged, united together in groups in the meshes of the eapillaries (Fig. 75). Finally, in adults the groups eonsist of a smaller number of eells, and many of them are quite isolated. The large eells which divide them appear to be partly united, resembling membranous layers, extremely simple and almost amorphous.

The arguments against the existenee of the pulmonary epithelium which have been drawn from the study of eomparative anatomy have all proved falsc in the light of fuller investigation. The pond-loach (*cobitis fossilis*) is a singular fish, whieh swallows

* 1, Capillary vessels. 2, Interstice in the capillaries (the white in the diagram is a portion of the capillary network; the dotted lines represent the meshes or interstices of this network). 3, Outline of the epithelial cells. 4, Nuclei of the cells, usually found in a mesh.

pulmonary emphysema ensues, a change which is so often observed in old people. This is not the case, however, in pathological conditions: when irritated, this epithelium becomes hypertrophied and proliferates. This is what gives rise to the false membranes in croup, and to the characteristic features of pneumonia; the alveoli are then entirely obliterated and transformed into a compact and resisting tissue, for which reason this state is known by the name of *hepatisation.* This epithelium has also the chief share in producing *tubercle*, and some other less common transformations, as *cancer of the lung.*

In cases of *infarctus* of the lung, especially when produced artificially in the dog, the epithelium may easily be seen to have undergone a certain hypertrophy in the pulmonary alveoli, infiltrated with blood, some of its cells falling into the alveolus, and mixing with the blood globules (Vulpian).

2. This epithelium is supported by a *membrane*, which forms a sort of *shell* to the alveolus. This consists of a connective tissue, which is nearly amorphous and full of plasmatic cells, and it has a large number of elastic fibres, forming a close network, the meshes of which are extremely minute. Sometimes the elastic fibres are found at a greater distance from each other, and, by dividing them, they may be made perfectly distinct in a preparation. These elastic elements, formed of fibres whose outline is strongly marked with numerous bifurcations, are of great importance in a physiological point of view; as, for instance, in *sputa*, these resist decay for a long time, and are often the only part of a necrosed and worn-out lung, which preserves the characteristic features that can be recognized by the microscope. In some animals this membrane is composed, in part, of smooth muscular fibres: it is not easy to decide, by anatomical examination, whether the case is the same in man.[1] We shall inquire later whether

air by the mouth, and, after having absorbed a part of the oxygen, gives off carbonic acid by the anus. Leydig could discover no intestinal epithelium in this fish, in which the respiration is partly intestinal; but Schmidt, by the aid of nitrate of silver, ascertained that the surface in question has a complete epithelial covering: here, too, the different cells are intermingled without any order, being sometimes of equal size and tolerably regular in arrangement, and at others grouped in such a manner that several small cells appear surrounded by smaller ones.

[1] "The muscular fibres appear in the large bronchi under the

this question can be solved by physiological experiments. This membrane is especially characterized by the large number of blood-vessels, consisting of a network of extremely small capillaries, so small as to allow only of the passage of a blood globule, and placed very close together, the meshes which separate them being exceedingly fine. It is found, for instance, that on a given surface of a pulmonary alveolus the space occupied by the capillaries amounts to three-fourths of the surface, and the intervals between them to only one-fourth. As the entire surface occupied by the alveoli amounts to two hundred square metres, it follows that the capillaries form an area of 150 square metres. This network is exceedingly fine and delicate, being only about the thickness of a blood globule; it nevertheless contains nearly two litres of blood. It has also been calculated that in twenty-four hours at least two thousand litres of blood pass through it; this network is thus continually renewed. These figures are important, as enabling us to form some idea of the magnitude of the gaseous exchanges which, we shall see, take place between the blood and the volume of air with which it is brought nearly in contact, being separated only by the thin wall of the capillaries and an extremely delicate epithelium.

We must, therefore, study the mechanism by means of which the external air is brought in contact with the respiratory surface, and see how it is renewed after the diffusion of gas between this surface and the blood has taken place.

These phenomena in every way resemble those of the digestion; but while the food received into the digestive tube must, before it can be assimilated, undergo a number of metamorphoses, the respiratory elements of the air are assimilated at once. The air simply undergoes a slight preparatory process, which brings it to the same state of temperature and of humidity as the pulmonary surface with which it is to come in contact. The origin of the pulmonary tree is so arranged as to render it inevitable that the air should undergo this slight modification: for the nasal

form of flattened, *circular* groups; these groups form a complete layer. As they are also found in branches of a size from $0^m.22$ to $0^m.18$, they probably extend to the pulmonary lobules." (Köl-liker, 1870).

This opinion as to the presence of the muscular element in the coat of the pulmonary vesicles was upheld by Moleschott, Piso-Borme, Hirschmann, and Chrzonszczewsky.

chambers are lined by an extremely moist mucous membrane, containing a large quantity of blood, and consequently very warm; it covers a number of folds (turbinated or spongy *bones*) in passages (*meatus*), through which the air, as it passes, is filtered, simultaneously becoming charged with moist vapor, and being brought to the temperature of the body. These considerations alone prove that respiration is naturally performed through the nose, and not through the mouth, and show the danger of breathing through the latter when in a cold dry atmosphere.

II. Mechanical Phenomena of Respiration.

The best method of exhibiting the arrangement of the circulating reservoir was presented by a diagram, and we shall find this plan equally useful in regard to the respiratory system. We see, in this way, that the air-bearing tubes, being placed side by side and the partitions left out, represent a very wide cone, having for its base the alveolar surface which we have already studied, and for its summit the opening of the nasal chambers (Fig. 76).

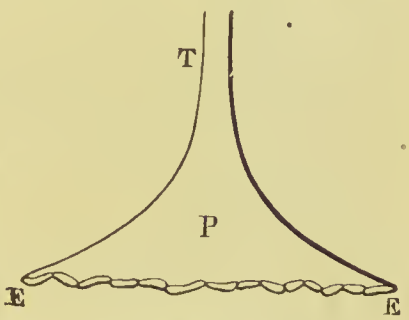


Fig. 76.
Diagram of the pulmonary cone.*

This arrangement shows us that when the air, no matter by whatever mechanism, enters or leaves this reservoir, the velocity of its current will be very different in the different zones of the cone, being more rapid as the zone is narrower (higher), and slower as the zone is wider (nearer the base); and that at the base of the cone, on the surface of the alveoli, the air is comparatively stagnant. In spite of the number of our respiratory movements, the air at the level of the breathing surface (alveolar) is never found pure, but contains as much as 8 per cent of carbonic acid, produced by former gaseous exchanges.[1] The upper part of

[1] The figure 8 per cent may appear too high, and yet there is no doubt that it is below the truth. Gréhant made it 7.5 per cent by direct experiment, but he did not analyze the gas which is in immediate contact with the respiratory surface; because, as we

* T, Trachea. P, Cavity of the lung. E, E, Respiratory surface (pavement epithelium of the alveoli.

the cone contains air nearly resembling atmospheric air: the air in the middle zones is less pure than this, but less degenerated than the first, containing only $\frac{4}{100}$ of carbonic acid.[1] Thus it rarely happens that the respiratory blood network comes in direct contact with ordinary atmospheric air.

Gréhant, replacing atmospheric air by hydrogen, succeeded in determining how many respiratory movements are necessary for the gas and the former contents of the lung to be so mingled as to become homogeneous. These experiments show that at least four or five successive respiratory movements are required to renew the gas contained in the pulmonary cone. By giving a certain quantity of hydrogen to a person to breathe, and then, in a series of experiments, analyzing the gas from the first, second, and third expiration, etc., Gréhant found that it is generally only after five inspirations and expirations, made in a receiver full of hydrogen, that this gas is uniformly spread throughout the lung. These experiments are extremely exact, for the blood scarcely absorbs any hydrogen (the difference made by absorption being scarcely $\frac{1}{28}$).

The introduction of air into the respiratory cone and its expulsion take place by means of the respiratory movements of inhalation and exhalation.

A. *Inhalation.*

The movement, by means of which inhalation takes place, consists in increasing the distance between the base and the

shall see later, this gas cannot be exhaled, the lung being never entirely empty: he analyzed those layers only which precede the one in question, and we may therefore infer that the proportion of carbonic acid in this latter must equal or even exceed 8 or 9 per cent. Gréhant's experiment is as follows: 500 cubic cent. of hydrogen are inhaled, and then immediately two exhalations are made, the second into a small india-rubber bag, furnished with a stop-cock, from which the air is entirely excluded by compression and by the presence of a small quantity of hydrogen, previously introduced. If the gas collected in this bag be analyzed, as the hydrogen is replaced by common air, it is found to contain 7.5 per cent of carbonic acid, 13.5 of oxygen, and 78.6 of nitrogen.

[1] Becher and Holmgren, by sounding the lung with a probe, extracted the air from the bronchi (middle zones of the pulmonary cone), and found it to contain carbonic acid in the proportion of 2.3 per cent. (See T. Strauss, "Des Travaux Récents sur les Gaz du Sang et les Échanges Respiratoires." (Archiv. Génér. de Médecine, 1873.)

summit, and also enlarging the other dimensions of the cone by separating its walls and pulling out the surface of the base. This produces a difference between the pressure of the exterior air and that in the respiratory cone, and also between that of the different layers of air in this cone, causing the interior and exterior gases to mingle more closely together.

This dilatation of the pulmonary cone takes place by means of the *cage of the thorax*, of which the diameter is increased by the contraction of the muscles and by the working of the bony levers of which it is formed. The wall of the thorax is composed in front and at the sides of the sternum and the ribs, and of the diaphragm below.

The *ribs* are *bony arches*, sloping from top to bottom, from back to front, and from within to without; so that when they rise, having as a fixed point their posterior extremity (costo-vertebral articulation), their anterior extremity is thrown forward, and their external convexity thrown outwards, causing an increase in the antero-posterior and transverse diameter of the lung: the Fig. 77 will better illustrate this mechanism than any explanation. The sternum must obviously move freely away from the vertebral column: the sternum and the vertebral column, being joined by the ribs, form, as it were, the two supports of a ladder with oblique rounds, and as these rounds become horizontal, the distance between the two supports increases; the forcible dilator of the urethra employed by surgeons constitutes a similar apparatus. Finally, the inclined plane formed by the rib sloping downwards and outwards, turns as it rises, about an oblique axis extending from the sternum to the vertebral

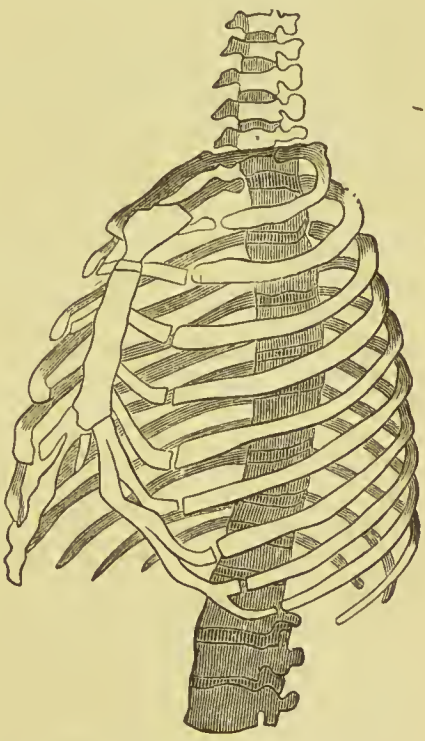


Fig. 77. — Thoracic cage *

* Vertebral column, with the ribs attached (dorsal region). These ribs extend to the front, where they join the sternum (directly, in the case of the seven upper ribs).

column, and representing the cord of the bow formed by the rib: the convexity of the rib is thus turned outwards, causing a transverse dilatation of the thorax.

The muscles which communicate these motions to the ribs are well known; they are those of the walls of the thorax, and their action is demonstrated by simply studying the direction of their fibres. They do not always act, however. When the breathing is calm, as it usually is, contraction of the intercostals, the scaleni, and, perhaps, a portion of the serratus magnus and of the serratus posticus superior, etc., will suffice; but, if the inspiration becomes forcible, and, as it were, constrained, we find (in cases of dyspnœa, for instance) that the sterno-cleido-mastoideus, the pectoral, the latissimus dorsi, and those muscles in general which, acting from a fixed position (especially when the arms are elevated and fixed) serve to raise the ribs and the sternum; all these come in play as re-enforcements. We shall also see that the diaphragm even may assist in the elevation of the ribs.

The working of these muscles may be easily observed in a single anatomical inspection. This is not the case, however, with the *intercostal muscles*, which have always been a subject of keen discussion among physiologists. We know that these muscles are divided into *internal intercostal* and *external intercostal* muscles, the fibres of each arranged crosswise. Every possible suggestion has been made as to the mode of action of these muscles, which have been thought to possess the power of inspiration and expiration, or one or the other only.[1] To our mind, the intercostal muscles per-

[1] Beau and Maissiat (Archives Générales de Médecine, 1842, 1843) have drawn up a curious list of the theories entertained as to the functions of the intercostal muscles. The ten theories have each been defended by numerous physiologists from Hamberger and Haller to Beau, Maissiat, and Sibson. Since that time (1843) other physiologists have taken part in this still undecided and apparently fruitless discussion. These theories may be summed up, by dividing them, as is done by Sappey, into six classes: 1. *The external and internal intercostal muscles are both inspiratory:* Borelli, Senac, Boerhaave, Winslow, Haller, Cuvier, Duchenne (de Boulogne), Marcellin Duval. The latter bases his opinion on experiments made on executed criminals a short time after death, when the muscles were still excitable. Duchenne (de Boulogne) rests chiefly on clinical observations made in cases of paralysis, in which respiration was kept up, in spite of the respiratory muscles being paralyzed, showing that active inspiration must have taken place by means of the intercostal muscles. We remark, in all the

form neither of these two functions: their principal office being to complete the wall of the thorax by filling up the intercostal spaces. It may be asked, however, if this could

cases of progressive atrophy reported by Duchenne, that no mention is made of the levatores costarum (*surcostaux*), a subject on which physiologists disagree as much as on that of the intercostals. Duchenne gives no opinion either way, and it appears probable that we shall be right in supposing the continuance of respiration to be due to the persistence of these muscles. 2. *They are both expiratory:* Vésalius, Diemerbrock, Sabatier. This is the opinion held by Beau and Maissiat: according to them the intercostal muscles come in play, especially when complex expiration takes place (as in screaming or coughing); at such times, in vivisection, the fibres of these muscles straighten and become tense, while in inspiration they are depressed and look inwards towards the lung. These physiologists adduce, in favor of their theory, an argument drawn from comparative physiology: "The respiration of birds is known to differ from that of the mammalia; expiration in birds is the active, and inspiration only the passive, result of the elasticity of the ribs, which spread apart, after having been pressed together by the action of the expiratory muscles. Consequently, the intercostal muscles, which exist in birds as well as in the mammifera, are affected only in expiration. We cannot believe that those muscles which are expiratory in birds are inspiratory in the mammifera." 3. *The external intercostal muscles are expiratory, and the internal inspiratory:* Galien, Bartholin. 4. *The external intercostal muscles are inspiratory, and the internal expiratory:* Spigel, Vesling, Hamberger. This opinion is principally founded on study of Hamberger's diagram (see Fig. 78, and his explanation, given in the text). It has been somewhat modified by Sibson: "The external intercostal between the thoracic set of ribs are throughout inspiratory; those portions between their cartilages are expiratory, between the diaphragmatic set of ribs they are *inspiratory behind*, *expiratory* at the side and in front, and between their cartilages they are inspiratory; between the intermediate set of ribs they are for the most part *slightly inspiratory* between the ribs, and *expiratory* in front between the cartilages." ("Mechanism of Respiration: Philosophical Transactions," 1847). Though this theory seems to involve us in confusion and trifling distinctions, if considered in a general point of view, we shall find, with Hermann, that it leads to a simpler conception than at first appears: "The external muscles are inspiratory in the bony parts of the ribs, and the internal in the cartilaginous. *As, however, this is almost the chief action of the two directions of the fibres, the intercostal may, in general, be classed among the inspiratory muscles*" (Hermann). 5. *The external and internal intercostal are at once inspiratory and expiratory:* Mayow, Magendie. 6. *The two intercostal muscles are passive in the movements of inspiration and expira-*

not be done as well by the fibrous tissue. The presence of the muscular tissue is explained, if we remember the general properties of muscle, which is the most elastic tissue of the whole economy. In this case a tissue of peculiar elasticity is required, the dimensions of the intercostal spaces changing incessantly in movements of the thorax. A tissue was required which would remain tense between the ribs, which would not be depressed from without inwards by exterior pressure during inspiration, or from within outwards by intrapulmonary pressure during expiration. This function is so important that, in order to fulfil it, the elasticity of the muscular tissue of the intercostal muscles must be kept in constant repair by nutrition; for instance, if, in pleuritis, inflammation has extended to these muscles, they become powerless to perform their appointed function, and in such cases an autopsy shows the lungs transversely grooved, having received this impression from the intercostal spaces, which then become capable of making this depression.

The necessity of preserving a constant elasticity of the intercostal spaces explains, finally, the existence of two layers of muscles, the external and the internal intercostal muscles. A simple diagram of the direction of these muscles (called Hamberger's diagram, Fig. 78) shows that, as the ribs descend (in expiration), the distance between the points of insertion of the intercostal muscles increases; and, again, diminishes as they rise (in inspiration): the reverse takes place in the case of the internal intercostal muscles. From this fact conclusions have been drawn as to the effect produced by the contraction of these muscles, the external being considered as elevating or inspiratory muscles, and the internal as depressing or expiratory (Hamberger). This diagram may be more clearly explained, however, it seems to us, by saying that the elasticity of the external intercostal muscles is brought into play during expiration, and that of the internal intercostal during inspiration. This alternation of elasticity in the wall is quite indispensable; because, in inspiration it is depressed from without inwards, and in

tion, and perform the office of a resisting wall: Van Helmont, Arantius, Cruveilhier: rather, they contract, not to produce the movements of inspiration and expiration, but in order, when they do occur, to resist the pressure of either the exterior or interior air (Küss). (See Aug. Jobelin, "Etude Critique sur les Muscles Intercostaux." Thèse de Strasbourg, 1870, No. 287.)

expiration from within outwards. We can also understand how, in violent efforts of respiration these muscles contract, not, however, in order to move the ribs, but to support the thoracic wall which their elasticity alone would be powerless to keep tense the spaces between the bony arches. Hamberger's diagram, in this point of view, shows contraction of the external intercostal muscles during inspiration, and of the internal during expiration.

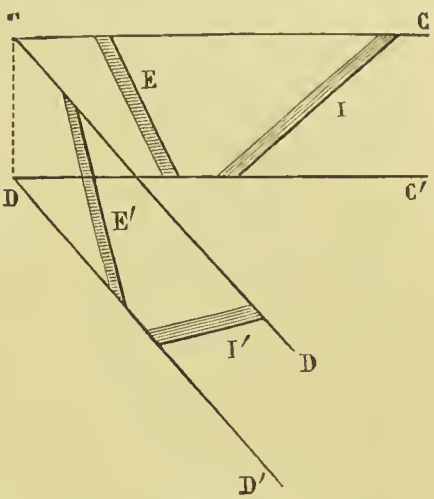


Fig. 78.
Diagram of the intercostal muscles.*

The intercostal spaces are not the only part of the thoracic wall in which the muscular elements are so arranged as to resist the changes of form induced by variations in pressure: in forcible inspirations, depressions, *supra-sternal or supra-clavicular depression*, are produced at the summit of the thoracic cage, the base of the neck. It is in these very parts that we find muscular layers (subcutaneous) or muscular bands (omohyoid) leading from the aponeuroses, and thus resisting the pressure from without inwards, especially in yawning, sobbing, etc.

We see, in short, that the transverse and antero-posterior diameters of the chest are increased by the play of the costal arches, set in motion by the contraction of a great number of muscles, some of which are constantly in play, while others are only accessory, and made use of in cases demanding extraordinary power; other muscles, the intercostal, in particular, serve only to keep the walls of the thorax in shape: in normal respiration their elastic properties alone suffice to produce this effect, but their contraction is necessary in *labored breathing.*

The enlargement of the vertical diameter is accomplished by means of the *diaphragm.* This muscle forms the base of the thoracic cone, and, as this descends, considerably modifies the capacity of the cone: its action exactly resem-

* Diagram known as Hamberger's.
C C, D C′, Ribs raised. C D, D D′, Ribs lowered. I I′, Internal intercostal muscles, extended when the ribs are raised (I), and relaxed when the ribs are lowered (I′). E E′, External intercostal muscles, extended when the ribs are lowered (E′), and relaxed when the ribs are raised (E).

bles that of a *piston* in the *cylinder of a pump*. This muscle, it is true, has the form of an arch, and it has been thought that in contraction its curve is straightened, and, in this way, enlarges the vertical diameter of the cavity of which it forms the base. This base is represented to be convex upwards during the repose of the muscle, and flat during its contraction. It must, however, be remarked that the curvature of the diaphragm exactly coincides with that of the abdominal viscera, as, for example, on the right, with that of the liver; thus, when the muscle contracts, it has no power to modify this convexity or curve, but can only cause it to change its place from top to bottom, driving the viscera before it in the same direction; thus we see the abdominal walls rise synchronically with each inspiratory dilatation of the thorax. The diaphragm thus constitutes a *piston having a convex form*, working in the cylinder of a pump formed by the thoracic cage; in descending, however, it does not act only on the vertical diameter of the thorax. We must remember that its circular edge is inserted in the ribs, that these latter are movable, and that, consequently, *when the arched centre of the diaphragm is directed downwards, its circular edge is sensibly elevated;* in other words, this muscle, like many others, has no really fixed points of insertion, and its fibres, as they contract, present at one time a relatively fixed point on the ribs, in order to lower both the phrenic centre and the viscera, and on the viscera (phrenic centre), in order to raise the ribs and the sternum.

By this action the diaphragm forces the ribs forward and outward, and, at the same time, dilates the thorax in its antero-posterior and transverse diameters; it may, therefore, be said to act at once on the three diameters of the chest. Most of the movements made in inspiration, especially in young subjects and in man,[1] proceed from the diaphragm; women, after attaining the age of puberty, form an exception to this rule, the respiratory type, instead of being *abdominal* (diaphragmatic) or *costo-inferior*, being rather *costo-superior*. This fact has, no doubt, some connection with the genital

[1] Paralysis of the diaphragm causes the greatest possible derangement in all those functions which require that the thoracic cage should be in perfect working order; although phonation is not destroyed, the voice becomes extremely weak; coughing and sneezing greatly hinder respiration. (See Duchenne (of Boulogne), "De l'Électrisation Localisée." Paris, 1872, p. 908.)

functions at the time of gestation, as the diaphragm could not then, without injury, press upon the gravid uterus.

In short, in inspiration the thorax is dilated in every direction, the action of the diaphragm serving chiefly to produce this effect. In making the complete inspiration which is necessary when some extraordinary effort is demanded, all the inspiratory powers, and all the mobility of which the ribs are capable, are brought into activity; the sternum is also raised by the muscles inserted at its upper extremity. But, under ordinary circumstances, when the breathing is quiet and unconsciously performed, it is found that, in the same person, some of the ribs possess an extraordinary freedom of movement, while others are nearly motionless, and that in the case of different persons, under similar conditions, the same ribs are not always found to be influenced by movements of the greatest extent. In some cases, also, the whole thoracic cage seems nearly motionless, no movement of the ribs can be detected. These facts have led to the establishment of three types of respiration (Beau and Maissiat): the abdominal type, the costo-inferior type, and the costo-superior. In children, of both sexes, respiration is *abdominal* (see above); in man, it is *costo-inferior;* in woman, it is generally *costo-superior.* This distinction, however, must not be looked upon as absolute: the diaphragm, even when it acts alone, evidently raises the lower ribs; in the costo-superior type, on the other hand, the lower ribs are also elevated to a certain degree, the sternum being unable to move without drawing them as it rises.

What is the state of the lungs during these movements in the thorax? We have seen that the pulmonary cone communicates with the exterior air: between the external surface of the lung and the internal surface of the cavity of the thorax, however, there exists a cavity, entirely closed, which is called the pleural cavity. By means of this empty space, the lung adheres to the cage of the thorax, and follows its every movement, exactly as a stone to which a piece of moistened leather is fastened by suction, follows the leather, when it is lifted up: this well known child's toy, exactly represents the mechanism, by means of which the thoracic cone, being actively enlarged, forces the pulmonary cone to follow all its changes in size, and, in short, to dilate. This is the mechanism of inspiration: the lung is quite passive; the thoracic cage dilates actively, and the lung is obliged to follow suit.

The effect of this mechanical phenomenon is to introduce a certain quantity of air into the lung. Indeed, the principle which governs the movements of the gases in respiration is the same as that which regulates the circulation of the fluids; that is to say, the consequence of *inequality of pressure.* From the moment when, by means of the enlargement of the pulmonary or thoracic cone (we shall, in future, regard these two words as synonymous), the gases in the pulmonary reservoir are rarefied, a blast of air rushes in from the exterior, as the lung is in free communication with the air, and this produces a current from without inwards. We have already observed that the velocity of this current differs, in different zones of the respiratory reservoir, owing to the form of the pulmonary cone (see p. 287).

B. *Expiration.*

All this is, however, only a part of the act of respiration: the introduction of air, or inspiration, is quickly followed by expiration or the expulsion of air by a current flowing in a contrary direction.

This latter movement takes place by means of a mechanism which differs entirely from that already described, and, in the normal condition, does not require the intervention of any extra-muscular effort. In order to form a clear idea of it, we must remember the exact structure of the pulmonary parenchyma, and the properties of its tissue. The envelope of the alveoli is formed of elastic tissue; it may, perhaps, contain some muscular tissue; but, if this be so, the latter very seldom gives rise to any phenomena of contraction.[1] On this point experimenters are not agreed. Williams made the experiment of passing an electric current through the lung of a dog, the bronchus being connected with a manometric apparatus; and observing the variations which took place in the column of mercury under the influence of the current he found that there was contraction of the smooth muscular fibres, either of the lung properly so called (alveoli), or of the bronchi. We have repeated this experiment several times without success, but, in spite of our failure,[2]

[1] The name of *muscles of Reisseisen* is often applied to these muscular fibres, they having been first described by this author. (Reisseisen, "De Fabrica Pulmonum." Strasbourg, 1822.)

[2] Paul Bert (Leçons sur la Physiologie Comparée de la Respiration Professées au Muséum d'Histoire Naturelle." Paris, 1870), having made a number of experiments on the contractility of

we are induced to believe that contraction of the pulmonary muscles takes place in man in certain morbid conditions, as in some forms of asthma or of pulmonary spasms, which appear to be caused, either by paralysis or spasms of these muscles (the alveoli and the small bronchi). The contraction of these muscular elements seems, however, to be of no great importance to the normal mechanism of respiration. We would not be understood to say that the muscular tissue is of no service. It must not be forgotten that the *elasticity* of the muscle forms as important a property of this tissue as its contractility, and is as useful to the economy; we have already seen, for instance, that the elasticity of the intercostal muscles is of more service than their contraction. The muscular tissue which enters into the construction of the lungs, as it appears to us, forms an elastic element, resembling, physiologically, the elastic tissue, properly so called. We need not pursue the subject farther here, having already enlarged upon it, in reference to the structure of the arteries.[1] If the lung is an eminently elastic tissue, it must, like the arteries, have a natural form to which it has a constant tendency to return. We shall see that this is the case, and also

the pulmonary tissue, deduced from them the following conclusions: the pulmonary tissue is contractile in mammals and in reptiles. This may be witnessed by means of galvanization with an induced current, after having fastened the trachea, and applied at the opposite extremity of the lungs two large metallic plates to serve as conductors. The manometric elevation which then takes place is not due to contraction of the œsophagus (as was supposed by Rugenburg), for it is seen even when the lungs have been extracted from the thorax, and when the heart and the œsophagus are removed. These contractions are, however, dependent on the pneumo-gastric nerve. It is very evident, on the other hand, that this contractility is of no great physiological importance; if these muscles came into play at every respiratory movement, they would contract more than twenty thousand times in twenty-four hours, a velocity which would entirely contradict what is positively known as to the general physiology of the smooth fibre. It is also plain that the contraction of the lung is far too slight to be of any service, in expiration particularly. It may, perhaps, govern some kind of peristaltic movement of the bronchi, by means of which the air is mixed together (Paul Bert). Finally, it is by no means an essential feature of the pulmonary parenchyma and of the respiratory functions, for section of the nerves, which entirely does away with it (section of the pneumo-gastric), causes no derangement in the lung in this respect (P. Bert).

[1] See p. 152, and the note on p. 154.

that, as with the arteries, this form is never completely attained during life. If the thoracic cage of a dead animal be opened, the lung is seen in the form of a spongy mass, lying firmly retracted towards the vertebral column; this is not, however, the natural form of the lung: the muscular tissue in a corpse has lost its elasticity, and the elastic tissue alone remains in a physiological state. If, again, we open the thoracic cage of a living rabbit, we find that the lung immediately retracts towards the vertebral column, in a much more remarkable degree than in the dead body; it is reduced to a small substance containing little or no air or blood, a compact parenchyma, hepatized, we might say. Should an abundant effusion, filling one of the pleural cavities, oblige the corresponding lung to retract on itself, we shall find that it retracts as in the foregoing experiment. In the case of the lung of a fœtus which has not breathed, strong points of resemblance to those here mentioned may be observed.

The *natural form* of the lung is thus that of a sponge, a bladder with numerous partitions, firmly retracted against the vertebral column; but, from the first inspiration of the fœtus, at birth, *this form is prevented;* the thorax dilates, and, by means of the pleural cavity, forces the lung, as we have already seen, to develop in a cavity represented in the diagram as a cone. From that moment, on account of the rigidity of the ribs, the lung can never (unless in the case of perforation or effusion of the pleura) attain its natural form, although it is always approaching it, exactly as we saw in the case of the arteries.

Inspiration, as we have studied it, may be considered as a *fresh violence* done to the lung, opposing to a greater degree its natural form.[1]

From this point of view it is easy to comprehend the *mechanism of expiration:* as soon as contraction of the inspiratory muscles ceases, the *pulmonary elasticity* which till then has been opposed, *re-asserts itself;* the lung retracts on itself, drawing with it, on account of the pleural vacuum, the wall of the thorax. It thus appears that, contrary to what takes place in inspiration, the lung is active, and the wall of the thorax passive; but, in reality, both these organs are passive. The diaphragm will act in the same way; if

[1] See L. Oger, "Considérations Physiologiques sur la Forme Naturelle de Certains Organes. Thèse de Strasbourg, 1870, No. 283.

the abdomen be opened and emptied, and the lower surface of the diaphragm examined, it will be found to have ascended automatically, as it were: this is because the lung has a tendency to ascend quite high, and draws the diaphragm forcibly with it, by means of the pleural vacuum, which obliges the diaphragm to follow the lung as we saw that the lung followed the diaphragm. Thus, in a corpse, the diaphragm is found greatly arched at the top, and very tense. Anatomists know well how favorable this circumstance is to the dissection of this muscle, but they also know that the slightest stroke of the scalpel, by which it is divided and the air allowed to enter between the two folds of the pleura, immediately causes the muscle to descend, when it becomes flabby, loose, and no longer capable of being handsomely dissected.

In the normal condition, therefore, the mechanism of inspiration and expiration is entirely different; the former is *active*, and is produced by muscular contraction; the latter is *passive*, and is dependent on phenomena of elasticity on the part of those organs which have been opposed by inspiration; for it is not the elasticity of the lung alone which produces this reaction, that of the walls of the thoracic cage, which have been equally opposed, must also be taken into account; the costal cartilages, for instance, which during inspiration are twisted around their axis in a rather remarkable manner. Finally, the viscera and the walls of the abdomen, having been displaced during inspiration, return to their original position, while the stomach and intestine, which contain elastic gases, by this means force the diaphragm upwards.

Expiration may, however, be active in certain cases. As we have seen that there is a *natural*, and a *forced*, *inspiration*, so we find that there is a *natural*, and a *forced*, *expiration*; in the latter only do the muscles come into play, those, namely, of the abdomen, the serrati postici, and, in general, all those by which the ribs can be depressed. This *active expiration* takes place especially in coughing: the walls of the thorax then no longer simply follow the lung as it draws back, but compress it, thus increasing the rapidity and energy of the expiratory current of air.

We cannot lay too much stress upon that special function of the pleural cavity by which, while it permits the lungs to move along the inner surface of the thoracic wall, binds these two surfaces together, in such a manner that if the thorax expands, the lung expands also; and if the latter con-

tracts, the former contracts likewise. The pleural folds inside these two organs act by means of adhesion by the vacuum, in short, producing a sort of suction, resembling that of cupping-glasses. It therefore appears surprising that what takes place in a cupping-glass, and what physical laws would seem to render necessary, does not take place here, that is, an extravasation of blood or of serum, or permanent effusion. In studying the *general physiology* of the epitheliums (p. 193), however, we stated that this globular lining had the power to prevent such exudations; and we find, in this case, an epithelium to which this function is assigned. Pathological observations confirm this view of the matter: it has been observed that nearly all diseases of the pleura, in which effusion appears, are caused by more or less entire destruction of the epithèlium, or by a state of degeneration which interferes with the exercise of its natural function.

C. *Function of the air-passages in respiration.*

The air, being drawn, by the respiratory movements, into the lung, and then driven out of it, passes through the narrow portion of our pulmonary cone; that is to say, the nostrils, the nasal chambers, the pharynx, and the trachea with the larynx. All these tubes exhibit mechanical phenomena, accessory to those which we have just been studying in the lung.

The nostrils dilate actively, but only in deep inspirations, and when there is any sensation of dyspnœa; the nasal chambers exhibit no special mechanical phenomena; but we know that they perform an important office, as being the place where the inhaled air is prepared, by being charged with heat and steam.

On a level with the pharynx the air-tube crosses the alimentary canal; we saw, in studying the latter, how the upper and lower orifices are obliterated as the food passes (p. 225).

In some animals the communication between the air-tube and the alimentary canal are permanently closed: in the cetaceans the trachea communicates directly with the nasal chambers, through which alone the animal can breathe. In the case of the pachydermata, the velum of the palate forms at the larynx a half-ring; and the respiration is, consequently, exclusively nasal. The horse, too, breathes only through the nose, on account of the disposition of the velum of the palate and of the epiglotis, the latter reaching to the posterior

orifice of the nasal chambers. Consequently, when the facial nerve of a horse, which innervates the muscles of the nostril, is cut, the nostril becomes inert and collapsed, and, as inspiration or expiration takes place, acts like a valve; so that, even if the animal opens the mouth wide, he is asphyxiated, in spite of his efforts to breathe. This effect is peculiar to the horse, not appearing in the dog or any other animal which breathes through the mouth (Cl. Bernard). Finally, in the human fœtus, as well as in the fœtus of the dog, it is observed that the larynx extends a little higher than in the adult, exhibiting, up to a certain point, the same disposition as that which we have just described in the lower mammals.

The larynx, the trachea and its divisions, and the bronchi, form a ramified tube, which, like all the constituent parts of the respiratory system, is distinguished by its elastic elements. These are, first, its *cartilaginous rings*, which are incomplete behind; the space left open, however, at the back of these rings, is filled by longitudinal bands of *elastic tissue*, interlaced and anastomosed under the mucous coat. Deeper down, the loose ends of each ring are joined together by *smooth muscular* fibres; which continue as far as the last bronchial ramifications, so that the last cartilaginous nuclei, the remains of the tracheal rings, have already disappeared while the muscular fibres are still found, in greater numbers even, and more uniformly arranged, all around the smaller air tubes (see p. 281); these fibres (muscles of Reisseisen) do not contract at will. We may repeat, in regard to them, what we have said of the muscular fibres of the alveolar wall about which some doubt exists; for there may be other muscular elements in the lungs than in the small bronchi and the small vessels. It is difficult, if not impossible, to prove that these fibres contract in order to take a share in physiological actions. Their participation[1] in pathological phenomena is also doubtful, as, for instance, they do not contract with sufficient force to assist in coughing; the possibility of their intervention in asthma and bronchial spasms we have already noticed. At all events, what we must recognize in this element, as in the preceding, is an eminently *elastic* tissue, whose chief use pertains to this property. Thus the tracheal and bronchial cartilages resist the great changes of shape, and restore the tube to its original form, when this has

[1] See note 2, p. 296.

been violated; being aided in this action by the elastic and muscular tissues.

The action of the muscles of the neck gives to the trachea an ascending and descending motion, corresponding with the respiratory movements. *During inspiration the trachea descends;* its calibre increases, and the current of air passes through easily, without friction. *During expiration, it rises,* lengthens, and thus becomes narrower; the channel through which the air passes out, being narrower than that through which it entered, causes the air to circulate more rapidly, and increases friction against the sides.

The larynx has also a large share in producing the difference between the current of air which is inhaled and that which is exhaled. When we study this organ as a vocal apparatus, we shall find that it is composed chiefly of an antero-posterior aperture (glottis), capable of enlarging and of narrowing, *enlarging in inspiration, and narrowing in expiration.* The degree of this narrowing differs in different cases: when a person makes a muscular *effort,* as for instance in defecation, the opening is entirely closed; the air can then no longer escape, and is compressed by the thorax, which forms a point of support to the muscles which are concerned in the effort.

The object of the difference in the velocity of the current of air when inhaled and exhaled, is the expulsion of foreign bodies, or rather, of those mucosities which may be found in the respiratory tree. The column of air, in inhalation, passes too slowly and with too little friction to enable it to bring out the mucosities which adhere to the wall; the current of exhaled air, on the other hand, presenting the opposite conditions, drags these small collections of matter forcibly to the upper orifice of the air-vessels.

In *coughing,* the expiration is more sudden, and the preceding inspiration slower than the normal expiration and inspiration; the chief effect of coughing is thus to throw off the mucosities which obstruct the respiratory or air tubes.

This continuous and unconscious expulsion of the mucosities is also effected by the movements of the vibratile cilia with which the columnar epithelium of the entire bronchial and tracheal tubes (except at the level of the vocal cords) are furnished; the movements of these cilia are of such a character that they carry to the exterior all the little bodies deposited on their surface, conveying them as far as to the cavity of the larynx (see p. 190). It is here only that expul-

sion becomes voluntary, for it is only in the larynx that the foreign bodies or mucosities are perceived; lower down, the sensations produced by their presence are very slight, and give rise to no reflex actions. The larynx is the starting-point of the reflex or voluntary phenomena which produce expulsion by means of this same mechanism of varying currents of air, but only with much greater energy; it is here that *coughing* is produced, and, higher up (in the pharynx and the nasal chambers), sneezing; and higher still (in the nostrils), the action of *blowing the nose:* all these consisting in a slow inspiration through a dilated orifice, and a sudden expiration through an orifice, narrowed, either by the contraction of its own muscles, or by a more or less distant mechanism.

III. Physical and Mechanical Consequences of Respiration.

A. *Mechanical effects produced upon the lung.*

We have already studied the numbers representing the varying conditions of the blood in regard to the intra-pulmonary air; we must remember that the respiratory surface, whose area is equal to 200 square metres, is essentially represented by a blood network of 150 square metres; that this network represents a mass of 2 litres of blood; that this blood is so constantly renewed that 20,000 litres of blood pass through the lung in 24 hours (Fig. 79). We have now to specify the results of respiration in regard to the quantity of air brought in contact with the blood, and the numerical statistics of the agencies by which the air is renewed.

The pulmonary cone represents a reservoir, the total average capacity of which amounts to 4 or 5 litres, when filled as full as possible; that is, when the deepest inspiration is made; on the other hand, when the strongest possible expiration is made, there still remains in the lungs from 1 to $1\frac{1}{2}$ litres of residual air, which cannot be exhaled in any way, because the lung, as we have seen, can never quite attain its natural form. The difference between this second figure and the first represents the quantity of air which may be introduced into the lung and then driven out, by means of the most energetic respiratory movements: this is what is called the *vital capacity* (or *pulmonary capacity*, or, better still, *respiratory capacity*); it is equal to $3\frac{1}{2}$ litres. This figure is of some importance, for it indicates the magnitude of the

physical conditions of the gaseous exchanges, and thus forms, as it were, a measure of our life, since to breathe is to live: a large number of instruments have been constructed for the

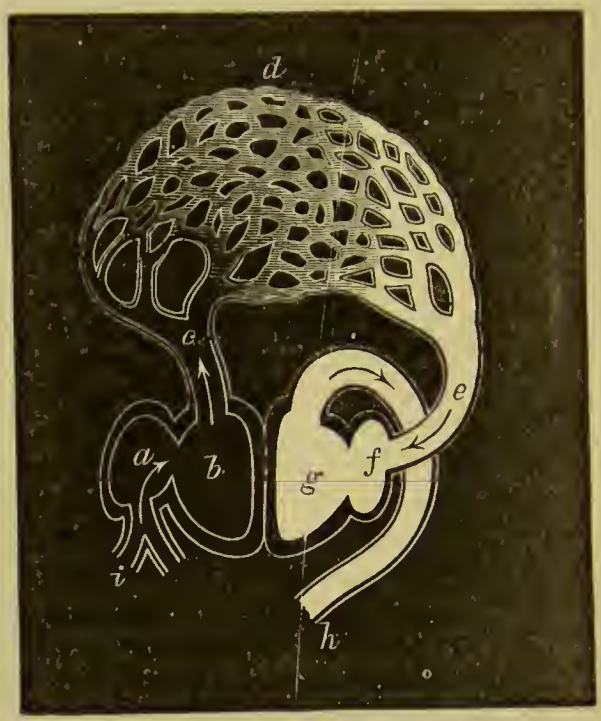


Fig. 79.—Circulation through the lung.*

purpose of estimating this amount; of these, the best known is Hutchinson's spirometer.[1] It consists simply of a gasometer

[1] Hutchinson, "Medico-chirurg. Transactions," 1846. More recently, the *anapnographer* of Messrs. Bergeon and Kastus (de Lyon) has been employed for comparative estimation. This instrument is, briefly, Marcy's sphygmograph, applied to currents of air which enter the chest or leave it at each respiration; it consists, chiefly, of a spring applied to the inspiratory and the expiratory current. A registering lever, furnished with a writing point, grows broader at the opposite end, and to this broader part a tube, into which the person breathes, is closely fitted. This part, which is an extremely light and delicate plate of aluminium, serves as a valve, kept immovable and vertical by two opposite springs of equal force, but moving with each respiratory current, and drawing after it the writing lever, which traces on the paper, first by vertical and

* *a*, *b*, Right heart (venous blood). *g*, *f*, Left heart (arterial blood). *c*, Pulmonary artery and its branches (carrying the venous blood into the lung). *e*, Pulmonary veins (rarely containing arterial blood). *d*, Vascular network of the lung. *h*, Aorta. (Dalton, "Human Physiology.")

immersed in a water receiver, and to which an india-rubber tube is attached, one end of which is placed in the mouth of the person experimented upon. The movements in the air-receiver are recorded by means of a movable indicator and a graduated and fixed scale. The person first takes a deep inspiration, and then breathes into the tube, and thus the maximum volume of the air inhaled is obtained. After experimenting in this manner on about 2000 persons, Hutchinson lays it down as a law that the maximum volume of air exhaled in the normal condition is in regular, if not mathematical proportion to the stature. In an athletic native of America, he found that the maximum volume of air exhaled was 7 litres (although the man died of consumption a few years after). We give (Fig. 80) a sketch of Schnepf's spirometer; it is only Hutchinson's instrument modified. The air, exhaled through the tube A, is received into the receiver C, which serves as a gasometer.[1]

The numbers given above represent extraordinary cases; in calm, ordinary respiration only one-half litre of air is introduced at each inspiration, and given out at each expiration. The latter may be called the figure *of normal respiration.*

then by horizontal lines, the movements of the valve, that is, the impressions which it receives, as well as the spring, from more or less intense or prolonged currents of air. The exquisite sensibility of this instrument, recording the slightest movements of the air, such as the bursting of a bubble in a flask, enables us exactly to determine the frequency of the respiratory movements, the relative length of each, their intensity, and, especially, their *form.* (Bergeon and Kastus, "Recherches sur la Physiologie Médicale de la Respiration, à l'Aide d'un nouvel Instrument, l'Anapnographe." Paris, 1869.) These writers have here made a collection of diagrams of remarkable accuracy, exhibiting special features, according to the age of the subject, the exaggerated exercise or morbid condition of the lungs, etc.

The spirometer, evidently, might be employed to ascertain the diminution in the pulmonary capacity at the beginning of phthisis, when physical signs (auscultation) leave the physician in doubt; but, for this purpose, it must have been previously measured in health. Any disease, such as emphysema, pleurisy, etc., which diminishes the space occupied by the air, or diminishes the quantity of air in circulation, produces the same effect as phthisis. Spirometry, therefore, cannot be said to be of any great use in medical practice.

[1] Schnepf, "Capacité Vitale du Poumon, ses Rapports Physiologiques et Pathologiques avec les Maladies de la Poitrine." 1858.

In order to ascertain exactly the capacity of the lungs, and the quantity of air introduced into them, the different portions of which this air is successively composed must be demonstrated: that portion of the air which cannot be driven out of the lungs by the most forcible expiration is called *residual air* (*a*); the air which may still be expelled after an ordinary expiration (though showing the difference between a moderate and a forced expiration) is called *air in reserve* (*b*); the air which we inhale and exhale at each ordinary respiration is called *the respiratory air* (*c*); finally, that quantity of air which we can inhale by means of a forcible inspiration (or the difference between normal and forced inspiration) is called *complementary air* (Hermann).

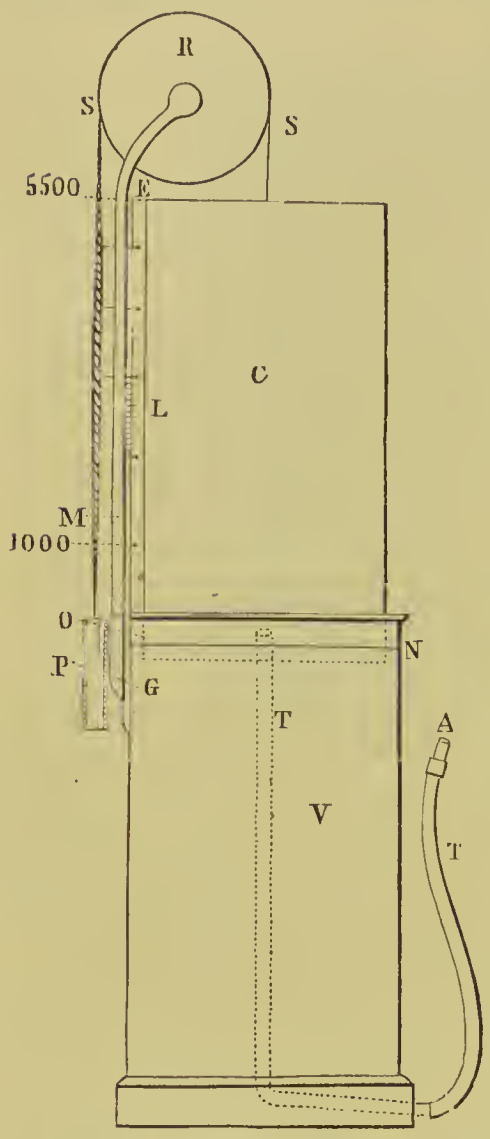


Fig. 80. — Schnepf's Spirometer.*

These names being accepted, nothing is easier than to estimate the last quantity (*d*) experimentally: the numerical value of the complementary air varies essentially with individuals, the diversity appearing to depend less on the size of the individual, than on the conformation of the chest. The quantity increases with the increase of the transverse diameter of the cavity of the thorax. The three diameters of the lung, or, what is the same thing, of the

* V, Brass cylinder. T T, Respiratory tube. A, Mouth of the respiratory tube. C, Receiver or gasometer. P, Balance-weight. S, Chain. R, Pulley. L, Scale. M, Upright bar. G, Case, supporting the scale. N, Surface of the fluid contained in the reservoir. E, Bottom of the gasometer. O, Open mouth of the gasometer.

thoracic cavity, differ greatly in importance, and, in this respect, the transverse diameter far surpasses the two others. (Sappey.)

The quantity *c*, or air of respiration (ordinary), may also be easily estimated: this is done by collecting the gas expelled from the lungs by a certain number of expirations, measuring it, and dividing the quantity thus obtained by the number of expirations. It is, however, difficult, during the experiment, not to change the number and extent of the respiratory movements. Gréhant, nevertheless, succeeded in obtaining perfect precision, by special controlling methods, founded on analysis of the air exhaled, at the beginning and at the end of the experiment;[1] he has thus estimated the quantity *c* at $\frac{510}{1000}$ of a litre, which is nearly the same as the standard $\frac{1}{2}$ litre (Dalton, Valentin, Bérard).

The other two quantities, air of reserve (*b*), and residual air (*a*), are much more difficult to determine: they can be measured only in a roundabout way. The sum of these two quantities ($a + b$) is first measured, and then that of one of them (*a*); the value of the third unknown (*b*) is obtained by subtraction.

Gréhant has estimated the sum $a + b$ with the greatest accuracy: his method is based on the same principle which we have already seen employed in estimating the quantity of blood contained in the circulating reservoir (see p. 111). In order to measure the blood contained in the vessels, we ascertain the degree of dilution which it undergoes by means of the injection of a certain quantity of water; in order to measure the volume of air remaining in the lungs after an ordinary expiration ($a + b$), the gases which are then contained in the respiratory tree or system are carefully mixed with a known quantity of hydrogen, and the analysis of the mixture is then made by means of the eudiometer. Thus, after an ordinary expiration in the air, the person making the experiment begins to breathe into a receiver, containing 500 cubic centimetres of pure hydrogen; after the fifth respiratory movement, the mixture is perfected, that is, it is exactly the same in the receiver and in the lung (see p. 288). It is only requisite then to analyze the gases in the receiver to obtain, by a simple calculation, the volume of air contained in the lung at the beginning of the experiment, that is, after ordi-

[1] See "Journal de l'Anatomie," etc., de Charles Robin, 1864, p. 542.

nary respiration, or, in other words, calculate the volume $a + b$. For persons whose ages are between 17 and 35 years, Gréhant obtained, in this manner, quantities varying between $2\frac{19}{100}$ litres, and $3\frac{23}{100}$ litres. (Gréhant calls this quantity the *pulmonary capacity:* this is not the meaning usually attached to this expression: if we refer to what was said above, we shall find that the *pulmonary* or *vital capacity* represents the sum $b + c + d$; while that settled by Gréhant represents the sum $a + b$.

The quantity a remains to be determined, and this, too, Gréhant enables us to do. "In order to decide this, I introduce a half-litre of air into a receiver (with a stop-cock); after an expiration made in the air, I inhale this gas, and then make as long an expiration as possible into the receiver: I then measure the volume of the exhaled gases; I find that is 1.8 litre. The pulmonary capacity ($a + b$, say 2.34 litres) is increased by the inspiration of $\frac{1}{2}$ litre, and diminished by 1.8 litre: what remains in the lungs is, therefore, 2.34 litres $+ 0.5 - 1.8$ litres $= 1.04$ litres." Thus the quantity a (residual air), which includes, it must be remembered, the volume of the buccal cavity, is about equal to *one litre.*[1]

The same experiment gives us the value of b, or the air in reserve. We have thus all the data necessary to solve the physiological problems relating to the quantities a, b, c, d.

One of the most important of these problems is that of the *ventilation of the lung*, which Gréhant was the first to solve. The quantity of fresh air, which, after each movement of ventilation, remains in the unit of volume in the ventilated space, is called the *coefficient of ventilation:* the lung is a space of this kind, and the respiratory movement really forms a ventilating movement. The coefficient of ventilation is, therefore, the quotient obtained by dividing the quantity (x) of pure air remaining in the lung after a normal expiration and inspiration, by the known volume of the lung after such expiration ($a + b = 2.365$ l., for instance). Gréhant discovered, by means of the inspiration of hydrogen, already mentioned, that the quantity $x =$ on an average 0.328 l. (that is to say that, when an ordinary inspiration or expiration is made, each

[1] We follow the example of most physiologists in calling this quantity "residual air," but we must forewarn the reader that Gréhant gives it the name of "air in reserve," a name which more naturally applies to the quantity b. (See "Revue des Cours Scientifiques." Août, 1871.)

being equal to a half-litre, about *one-third* of the air inhaled is given back to the atmosphere, while *two-thirds* of pure air enter the lung, and renew its contents by mixing with them). The *coefficient of pulmonary ventilation* is, therefore, $\frac{320}{2365} = 0.145$; or a little more than $\frac{1}{10}$. It varies, however, with the volume of the lungs, and with the volume of inspiration. Gréhant has obtained extremely interesting results from this point of view. Thus he found that an inspiration of $\frac{1}{2}$ litre renews the air in the lungs better than two inspirations of 300 cubic centimetres, forming, together, 600 cubic centimetres. "This is the reason that in certain affections of the chest, in which patients inhale frequently, but not deeply, the air is not renewed so perfectly as in the normal state; 40 inspirations, of 300 cubic centimetres each, not producing such entire renovation of the air as 20 inspirations of 500 cubic centimetres."

Such is the estimate of the quantities of air introduced into the lung: the frequency with which the movements producing this renovation of the air are performed is easily ascertained; we breathe 13 or 14 times in a minute, thus making the number of inspirations 20,000 in 24 hours; as each inspiration introduces $\frac{1}{2}$ litre of air into the lungs, we breathe altogether 10,000 litres of air in a day. The quantity of blood brought into contact with this air has a very simple numerical relation to it, being 20,000 litres, or rather 10,000 litres of globules (1 litre of blood $= \frac{1}{2}$ litre of globules, or *cruor* $+ \frac{1}{2}$ litre of *liquor*).

The *differences of pressure*, caused by the mechanical working of the thorax, and which are intended to produce the movements of the air, are also very slight in the normal condition: if, for instance, we represent the exterior pressure (atmospheric pressure), in the state of repose, by 100, the intra-pulmonary pressure will be 100 also. The dilatation produced by inspiration, however, causes the interior pressure to descend to 99.5, and thus the interior air penetrates the lung ($\frac{1}{2}$ a litre, as we have said). When the normal expiration occurs, the intra-pulmonary pressure rises to 100.5, and a quantity of gas equal to that which has entered the lungs, is thrown off.

In forcible respiratory movements, however, these figures are much larger: thus inspiration may reduce the interior pressure to 75, while expiration may increase it to 130 or 135; in other words, in a very forcible inspiration, the interior pressure differs from the exterior by $\frac{1}{4}$, and in forcible expira-

tion, by $\frac{1}{3}$ of that of the atmosphere. We see that the difference is greater in expiration than in inspiration, in the case of an energetic movement: as we know that more mechanical effect is produced, for instance, by blowing through a tube, than by inhaling through it. The reason of this difference is evident, if we remember that the contraction of the inspiratory muscles is impeded by the elasticity of a number of organs which are disturbed by such contraction (the lungs, costal cartilages, abdominal viscera, &c.); while the expiratory muscles, which are at least as powerful as their antagonists, have only to add their force to that of these elastic parts acting in the same direction. This power of forced expiration, joined to the mechanical conditions produced by the contraction of the trachea and the glottis, serve to promote the expulsion of foreign bodies, or mucosities (coughing).

We repeat that this difference, on the side of expiration, exists only in the case of forcible respiration: in the normal condition expiration is only a reaction of the elasticity of the organs overcome by inspiration; and thus one has nearly as much power as the other. But they are not both of the same type, the same form, or the same duration; that is to say, inspiration, produced by muscular contraction, takes place in a manner nearly uniform, and may be represented by a regularly ascending line; while expiration, on account of the way in which it is produced, follows, in its form, the same law as the elastic bodies: for instance, if we compress a gas in a

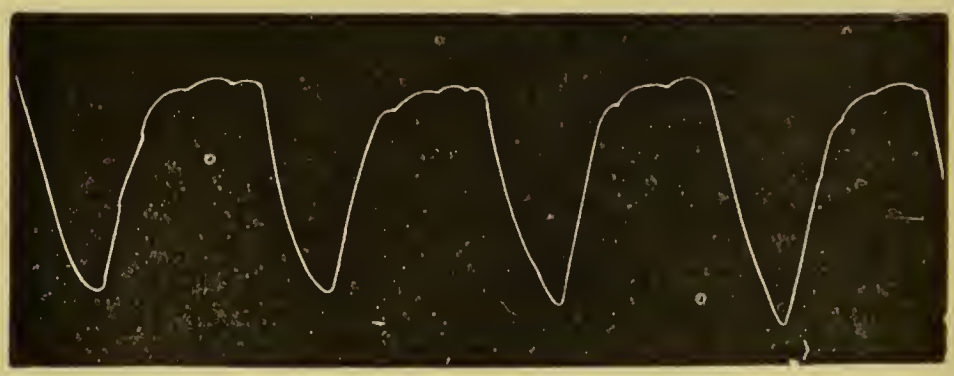


Fig. 81.—Normal kymographic tracings of the respiratory movements in man (Marey).*

syringe, by means of a piston, we shall find that the moment we cease to press the latter, it rises up, suddenly at first, but

* The descending line is that of inspiration, the ascending that of expiration, the pen moving from left to right.

afterwards the ascending reaction continues more slowly; the same is true with expiration, which, sudden at first, continues with a slow movement, lasting a considerable time (Fig. 82, 3): it may be represented in a diagram by a line descending suddenly, and almost vertically, and then by a very long and oblique descending line (Fig. 81 and 82). Thus expiration, in short, occupies a longer time than inspiration; a superficial examination, however, shows only the first period of expiration, which then appears extremely short, shorter even than inspiration.

The passage of the air through the respiratory tubes produces certain kinds of friction, and causes the inspiratory and expiratory murmur (*bruit*): the former sound lasts as long as the action producing it; the latter is usually perceived only during the first part of this action, the current of air

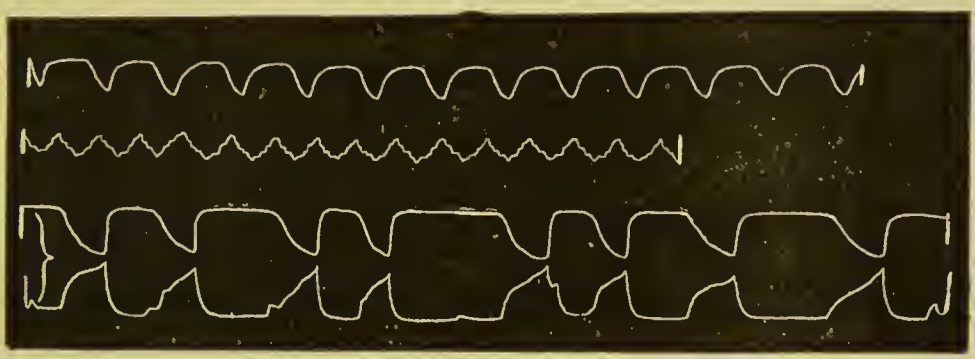


Fig. 82. — Kymographic tracings of the respiration of a dog.*

being too slow and feeble in the second part, to make itself heard. We see thus that auscultation of the normal respiration would give a false idea as to the relative duration of the two acts constituting respiration, by representing inspiration as occupying a longer time than expiration; what is true in regard to the sounds produced not being true in regard to the causes which produce them.

Since the discovery of auscultation by Laënnec many theories have been propounded which seek to explain the sound produced by normal respiration, and the changes which it

* The double line (3) especially represents the difference between inspiration and expiration. The respiration is recorded at the same moment in the trachea (by variations of manometric pressure) and in the thorax (the registering drum and lever being moved by the dilatations of the chest): these two tracings are contrasted for comparison. (P. Bert, "Leçons sur la Physiologie comparée de la Respiration.")

undergoes in pathological cases. The *respiratory murmur* is evidently caused by friction against the sides of the air-vessels, but it is not easy to decide exactly where this murmur is localized. It was formerly attributed to the unfolding of the pulmonary vesicles, whence the name of *vesicular murmur*. Beau, however, maintains that its seat is at the opening of the glottis; many physiologists have adopted this opinion, while Bergeon has recently (1869) combined the two theories, slightly modifying both. He holds that the inspiratory sound is produced in two places, the glottis and the lung, while the expiratory sound is produced in the glottis only; the former being caused by the passage of the air through the constricted orifices, this passage being accompanied by the formation of fluid, vibrating veins (see *Circulation*, p. 164); these veins are formed both at the glottis and at that of the opening of the small bronchi into the pulmonary alveoli. The cause producing the respiratory sounds cannot be supposed to exist only at the level of the glottis, for the sound continues the same in cases in which the air no longer passes through the larynx, as after operations in tracheotomy. We may, therefore, conclude that the causes of the *respiratory murmur* are manifold, and the principal one may be said to be (Sabatier) the dull crepitation produced by the detachment of the trabeculae, or slightly moistened partitions of the pulmonary alveoli; the vibrations made in the air at the sharp edges formed by the bronchial bifurcations; the friction of the air against the bronchial coats; and, finally, the more or less decided resonance of the superior or glottic sounds.[1]

B. *Mechanical effects produced by respiration in the organs adjacent to the lungs.*

The mechanical consequences of the inspiratory and expiratory movements are not confined to the air-vessels; the blood vessels and the circulation of the blood are also affected by these movements, the greater part of the circulating system being contained in the cavity of the thorax.

We have represented the circulation in a diagram, by the figure of 8, the upper half representing the pulmonary circulation, and the lower, the general circulation, the point of

[1] See "Les Nouvelles Recherches," de V. Cornil; "Anatomie Pathologique et Auscultation du Poumon." Mouvement médical, Avril et mai, 1873.

junction being occupied by the heart (see Fig. 42, p. 143); the cavity of the lungs contains: 1. All that portion of the circulation called pulmonary, that is, the upper circle; 2. The point of junction of these two circles, viz., the heart; and 3. The lateral origins of the lower circle, or the summit of the arterial and of the venous cone. The changes in intra-thoracic pressure affect all these three portions.

This influence is counteracted, however, in the case of the circulation of the *thorax*, by the fact that the venous cone of this circulation is subjected to the same variations, and simultaneously, as the arterial cone; and as the differences of intravascular pressure which produce the circulation remain the same, no change in the circulation occurs; the circulation is but slightly influenced, except by the more or less complete expansion of the alveoli, which occasions a greater or less permeability of the capillary vessels, or, in other words, of the base of the pulmonary cone.

The influence of respiration is much more sensibly felt in the heart: an expiration made with force, as in any great exertion, causes immense pressure upon the heart, and as the coats of this cavity are thin, and easily compressed, a deformation ensues. Weber has made experiments to show this, by first making an extremely deep inspiration, and then very forcible movements of expiration, the glottis being closed, and the arms kept fixed against his sides. After the lapse of a few seconds, a change is observed in the pulse, which becomes slower, and, at length, ceases entirely; if the ear is placed over the chest, no sound is heard, whence we may infer that the heart has ceased to beat. If the experiment be continued, the person loses consciousness, and thus, in spite of himself, returns to his original state of life and circulation.

If, however, the person remains passive, the stoppage of the heart continues, and may end in death; this is probably the case with persons who are squeezed to death in a turbulent crowd, the outside pressure being continued even after syncope has been produced.[1] In experiments or accidents of this kind, the stoppage is not the same in all parts of the

[1] A case has been reported by the American editor ("Boston Med. & Surg. Journal," Dec. 11, 1873, p. 577), in which a rupture of the right auricle was caused by compression of the thoracic walls. Another accident (reported in the "Gaz. Hebd.," March 27, 1874, p. 199, by MM. Doubre and Charpentier) of compression of the thorax between a wheel and the ground, resulted also in the rupture of the right auricle.

heart: it takes place chiefly in the right auricle. The effect produced may be shown by exposing the heart of a frog, and compressing it at the point of the opening of the vena cava, and thus preventing the entrance of the blood: the entire heart then ceases to beat, because the ventricle, as well as the auricle, receiving no more blood, there is no longer on the inner surface of these cavities any impression which may serve as a point of origin of the reflex action which causes the pulsation of the heart. If the man or animal, however, is in a state of perfect health, it is not very likely that this mechanism of compression will produce death. Indeed, though the heart stops, the arteries by means of their elasticity drive their contents into the veins, which become turgid, while the summit of the venous cone quickly pours into the heart a mass of blood, thus setting the heart in motion again. The mechanism which we have described, however, explains the so-called voluntary stoppage of the heart, of which some persons have professed to be capable: the will acts upon the heart, in this case, only through the medium of respiration.

Respiration produces a similar effect on the general circulation, the top of the two cones (the arterial and the venous) being included in the thorax. We know that at the top of the venous cone the pressure is so slight that it may be represented by 0 or $\frac{1}{100}$; at the top of the arterial cone, on the other hand, the contraction of the ventricle produces a pressure which may be reckoned as $\frac{25}{100}$ (see p. 143).

Let us suppose that, by means of a strong expiration, a pressure of $\frac{15}{100}$ is produced in the cavity of the thorax: the pressure at the top of the venous cone will then be $\frac{16}{100}$, an enormous pressure for this part of the circulating system, an essential feature of its working condition being the absence of all pressure. The consequence will be a considerable reflux into the veins; this reflux into the veins near the heart is prevented by the numerous valves with which they are furnished, and it is only at the top of the cone that the pressure is made. As the blood continues to flow, and finds an obstruction to its further progress, stagnation follows, accompanied by distention of the veins adjacent to the thorax. This is chiefly seen in straining, and in those processes which are accompanied by it, as parturition, defecation, &c.; the signs of the stagnation of the blood are injection of the eyes, redness of the face, cessation of the cerebral circulation, and, finally, the suppression of the functions of the brain (vertigo and even apoplexy): a state of less entire stagnation, often

repeated, causes dilatation of the veins, varices, vascular hypertrophy of the thyroid gland, &c.

This influence of expiration produces equally marked effects in the arterial cone. At the top of this cone, the pressure produced by the ventricle is $\frac{25}{100}$. If we assume the pressure in the thorax at $\frac{15}{100}$, in the arterial cone it will be $\frac{40}{100}$; this causes the arterial blood to flow much faster, there being here nothing which can counteract or delay the effect of this increase of pressure; and the fluid is forced into the arteries by two pumps, the heart and the thorax. It is true that the slackening of the flow of the blood in the veins has a tendency to counterbalance its increased rapidity in the arteries, but, in spite of this, immense pressure is produced on the entire current of the circulation, accompanied by a strong tendency to hemorrhage, ruptures of aneurisms, varicose dilatations, &c.[1]

The phenomena which follow a diminution of pressure in the thorax, produced by a violent inspiratory movement, are entirely different from the above. The pressure at the top of the venous cone then becomes less than 0, or, in fact, aspiration of blood by the veins, an increased acceleration of the circulation of the venous blood; if the blood does not flow in sufficient quantity to satisfy this aspiratory demand, the coats of the veins become relaxed, and show a tendency to collapse. In the veins which are near the thorax, and are especially under the influence of this aspiration, the relations between the coats of the veins and the aponeuroses are such that these vessels remain constantly open: the aspiration is thus continued to veins more remote from the heart. In a surgical operation, therefore, if one of the veins near the thorax be opened, the outer air, at the moment of inspiration, may be drawn into the interior of the vessel, an occurrence which is generally followed by speedy death.

Under the influence of this inspiratory aspiration, the aortic pressure, which is $\frac{25}{100}$, falls to $\frac{15}{100}$, or $\frac{10}{100}$, causing a slackening of the circulation, diminished tension of the vessels, feebleness of the pulse, &c. But while the conditions of expiration were favorable to hemorrhage, these resist it, and, in order to arrest the flow of blood, it is sometimes only necessary to cause the patient to make several deep inspirations.

These results, at which we have arrived by simple reason-

[1] See F. Guyon, "Note sur l'Arrêt de la Circulation Carotidienne pendant l'Effort." Archives de Physiologie, 1866.

ing, have been experimentally verified by Marey, by means of the graphic method. This physiologist has reached the following conclusions in regard to the effect produced on the circulation by respiration. Respiration affects the pulsation of the heart; it not only causes variation in the line of the whole tracing, but imparts to the pulsations produced during inspiration an amplitude and a form which differ from those observed during expiration; when respiration is stopped, the pulsation of the heart slackens and diminishes in intensity: these modifications are explained by the fact that the blood passes less readily through the lung when the latter is not in action. After an effort (forcible attempt at expiration, the glottis being closed) the pulsation of the heart assumes special features. The left ventricle makes its action intensely perceptible, while the blood in the auricle is violently precipitated at the period at which the diastole begins. If the person experimenting breathe through a narrow tube, the relation between the pulsation of the heart and the respiratory movements is changed: while the respiration becomes less frequent, the pulsations become more rapid.

We also find in the pulse differences corresponding to the different respiratory types (thoracic and abdominal types, see p. 295). The thoracic type exhibits a diminution of pressure during inspiration, the whole extent of the line traced rising again during expiration. The abdominal type produces exactly the contrary effect (Marey). We give (Fig. 83) a

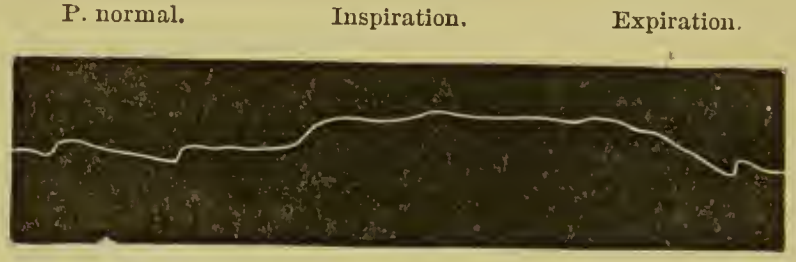


Fig. 83. — Abdominal type.

graphic tracing of the pulse, while respiration is taking place during forcible contraction of the diaphragm. We see that in the abdominal type (as in the thoracic) the pulsation diminishes, and, finally, disappears, while the arterial tension increases.[1]

We may mention, in conclusion, and rather as an experi-

[1] P. Lorain, "Etudes de Médecine Clinique." Le Pouls, 1870.

mental curiosity than as an important physiological fact, the influence, in a contrary direction, which may be observed to exist between the heart and the lungs. "We know that the pulsation of the heart changes the condition of the intra-thoracic pressure; supposing the thorax to be immovable, the afflux of blood which takes place at each diastole, should compress the air in the lungs, and, if the glottis is open, give rise to a slight expiration; in the same manner, when the heart is suddenly emptied, the blood which gushes out of the thorax is replaced by a certain quantity of air which enters through the trachea. In the normal condition, we are scarcely sensible of this, on account of the constant modifications produced by respiration in the respiratory capacity of the thorax. The fact, however, can easily be made plain, by placing the trachea of a dog in communication with the registering apparatus, and then puncturing or severing the medulla oblongata of the animal by a single stroke: respiration ceases immediately, while the heart continues to beat for some minutes, *its pulsations being registered through the medium of the air in the trachea*" (P. Bert).

IV. Chemical Phenomena of Respiration.

We understand how the air and the blood are brought into contact with each other, and also by what mechanism they are constantly renewed; we have now to examine the gaseous exchanges which are produced by this contact taking place in the lungs: what these are we shall see by ascertaining the changes made in the air and in the blood, during their passage through the lungs.

A. *Modifications in the air exhaled.*

We know that 10 cubic metres (10,000 litres) of air are received into the lungs daily, and that nearly an equal quantity is expelled: we thus retain about $\frac{1}{40}$ or $\frac{1}{50}$ of the air inhaled; at the first examination, however, the exhaled gas is found undiminished in quantity, on account of the vapor contained in it, which occupies a considerable space. A still more important change which takes place in the air is the loss of *oxygen*, which is replaced in a great measure by *carbonic acid*, one-fifth of the amount of the 10 cubic metres of air inhaled is oxygen (21 parts of O. to 79 parts of N.); this is equal by weight to $2\frac{1}{2}$ kilos. of oxygen. In the air ex-

haled in 24 hours, only 1 kilo. 750 grms. remains; that is to say, that 750 grms. of oxygen have been retained by the lungs (2.500 — 1.750 = 750). We see thus that we retain a sum total of ¾ of a kilo. (or 750 grms.) of oxygen in 24 hours (750 grms., or a volume of 500 litres).

On the other hand, we know that the carbonic acid is found represented by thousandths only in the atmospheric air, the air which we breathe ($\frac{1}{2500}$ or $\frac{4}{1000}$). The quantity found in the exhaled air is very large: but yet it differs, according to circumstances, though, on the average, we may be said to exhale 850 grms. of carbonic acid in 24 hours (a volume of 400 litres: in order to account for the diminution of volume which we have observed between the air inhaled and that which is exhaled, compare these figures with the 500 litres of O. absorbed.) These are the principal facts to be noted in regard to the air; the other changes which take place are unimportant. Thus air contains ⅘ parts nitrogen (21 of O., 79 of N.), the quantity of this gas inhaled and exhaled is supposed by some persons to be equal: others maintain that it varies, and that, at times, a little more than the usual quantity is given off, showing that a certain quantity is excreted by the lungs: indeed, traces of ammonia and various exhalations arising from nitrogenous substances are frequently met with in the lungs, as well as the vapors belonging to all those volatile matters which sometimes find their way into the blood, as, for instance, alcohol, ether, phosphorated products, and paludal gases.

B. *Modifications in the blood which passes through the lungs.*

What is the process which goes on in the blood? Experiments have proved, what our previous knowledge enabled us to guess, that the carbonic acid which is exhaled arises from the venous blood; the latter throwing off this excretory product, imbibes oxygen in order to pass into the state of arterial blood. We have already studied the gases of the blood, and have seen that, from the point of view of respiration, the blood may be looked upon as a solution of gas, the blood globule being the vehicle of the oxygen, and the serum that of the carbonic acid; we have also found that the essential difference between the arterial and the venous blood consists in the predominance of oxygen in the former, and of carbonic acid in the latter.

Recent analyses of the gases contained in the blood, give,[1]
In 100 parts of arterial blood (in a dog):
Oxygen — 20 parts, carbonic acid — 34.8 parts.
In 100 parts of venous blood:
Oxygen — 12 parts, carbonic acid — 47 parts.

The brilliant red color of the arterial blood may, perhaps, be caused by a chemical action of the oxygen on the coloring matter, or hematine, but it appears to be chiefly owing to a change of form: under the exciting influence of oxygen, as well as under that of some other agents (chloride of sodium, for instance), the blood globule becomes flatter and slighter, and refracts the light in a different manner from that seen when it is under the influence of carbonic acid; this latter has the effect of causing it to swell, and approach more nearly the spherical form.

In passing through the lungs, the blood also, as we have seen, gives off a certain quantity of vapor (the quantity varies, but may be assumed to be at least 300 grms. in 24 hours). The exhaled air, indeed, as it leaves the lungs, is nearly saturated with vapor, at a temperature which is nearly that of the body, as has been demonstrated by Gréhant: we have already seen that if a half-litre of atmospheric air be inhaled, the expiration which follows throws off one-third of this volume of pure air mixed with two-thirds of vitiated air. The vitiated air, which has been for some time in contact with the bronchi, is of the same temperature as the lungs, and is thoroughly moistened; but the third part of pure air which is immediately given back in breathing, not having remained sufficiently long in the respiratory tree to assume exactly the temperature of its walls, it follows that the entire quantity of air expelled has not the same temperature as the body. Gréhant has shown, by very close experimental researches, that, the temperature of the exterior air being 22° (C.), that of the air exhaled is equal to 35°.3 (C.), 17 expirations a minute: the exterior temperature being — 6° (C.), that of the air exhaled is only 29°.8 (C.) (Valentin). Gréhant has also shown that the air exhaled is surcharged with vapor at its own temperature, and not at that of the body, which is slightly higher (see animal heat).[2]

The blood, therefore, grows cooler as it comes in contact

[1] Ludwig and his pupils. Archiv. de Pflüger, 1872.
[2] N. Gréhant, "Cours de l'École Pratique." Revue des Cours Scientifiques, Novembre, 1871.

with the air of the lungs, by yielding up to it a portion of its heat.

This fact was long disputed; first, because direct experiment on the subject seemed to contradict it: two thermometers, placed, one in the left heart, and the other in the right, seemed to show an increase of heat in the former cavity, and a consequent heating of the blood in its passage towards the lung: more careful examination has, however, led to an entirely opposite conclusion (Cl. Bernard), and shown that, in former experiments, allowance had not been made for the inequality of thickness in the coats of the two ventricles, occasioning a greater loss of heat in the right ventricle (the coats of which are thin), than in the left (of which the coats are thick).[1] In the second place, the increased temperature of the arterialized blood was looked upon as the necessary consequence of the hypothesis that actual combustion takes place in the lungs, and that it is here that the oxygen absorbed during inspiration is employed to consume the carbon and produce the carbonic acid exhaled in expiration.

It is now, however, proved that the production of carbonic acid in the blood is not limited to the pulmonary surface, but occurs in the whole organism, throughout the current of the circulation, and, more particularly, in the capillary network: carbonic acid is, indeed, found everywhere in the venous

[1] Following experiments made recently, Heidenhain and Körner have sought to prove that the difference in temperature between the blood of the left heart and that of the right is not caused by the cooling of the blood in its passage into the lungs. They maintain that the blood is neither cooled nor heated in passing through the lungs, but that the higher temperature of the right ventricle is caused by its being situated more immediately in the phrenic centre, and, consequently, being in contact with the organs contained in the abdominal cavity (the liver, stomach, and intestines), which have all a higher temperature than that of the organs of the thorax. Cl. Bernard, however, opposes this theory by instancing those cases of *ectopia* (or displacement) of the heart, in which the heart from its transposition is not in contact either with the diaphragm or with the abdominal viscera, and yet contains warmer blood in the right ventricle than in the left. On the other hand, the heart of a dog, surrounded by its pericardium, and is in no way united to the diaphragm, floats in the chest, if we may be allowed the expression; by changing the position of this animal, the relation of the diaphragm to the ventricle is modified, without, however, changing the relation between the temperature of the blood of the two ventricles. (Cl. Bernard, Cours de 1872.)

blood, and only increases as we approach the summit of the venous cone. The respiratory phenomenon of the lungs simply consists in a gaseous exchange, resembling, more or less, the phenomenon of diffusion, but which is not combustion: combustion takes place at those points where the tissues of the organism come in close contact with the blood, and in the very structure of these tissues; the arterial blood is only the vehicle of the oxygen to these tissues, as the venous blood is that which carries off the carbonic acid.

C. *Theory of respiration.*

Respiration, therefore, considered, not from the point of view of the gaseous exchanges, but from that of the chemical phenomena of combustion, of combination and separation, — respiration in its very essence, in short, — takes place, not in the lung, but in the most intimate portions of the tissues; thus the liver, in which extremely important, though not well-defined, chemical phenomena take place, makes use of all the oxygen contained in the blood of the portal vein, while the blood which flows from the liver exhibits both the highest temperature and the most decided features of the typical venous blood. That the tissues themselves actually breathe, in a chemical sense, is proved by placing them in an oxygenized gaseous medium,[1] in which their respiration may be seen directly: thus, if a muscle be detached from an organism, and suspended in an oxygenized atmosphere, it will consume oxygen, and exhale carbonic acid: this combustion is still more intense if the muscle be made to contract, the reason of which will be understood by referring to the physiological study of the muscle. In its natural position in the organism, the phenomena of the muscle are the same as those of the other tissues; with the exception that the blood here performs the office of a medium from which the living element borrows oxygen (arterial blood), and gives back carbonic acid (venous blood). Thus the blood of the veins of a muscle is much darker, more venous, in short, when the muscle is contracted than when it is in a state of entire repose.

Respiration consists, then, in man and the superior animals, considered in a general way, of three principal parts, three

[1] See P. Bert, "Leçons sur la Respiration." Leçons 3 and 4: *Respiration des Tissus.*

phenomena closely connected and dependent upon each other: 1, Respiration of the tissues; 2, Functions of the blood as a vehicle of the agents and of the gaseous products of the respiration of the tissues; 3, Gaseous exchanges of the blood at the pulmonary surface. Modern investigation has thrown great light on the inner phenomena composing each of these great acts, the study of which, in the series of organized beings, clearly shows their relative importance.

1. *Respiration of the Tissues.* We have already spoken several times of the respiration of the tissues (see pp. 320 and 321): as the anatomical elements breathe when separated, so we see that inferior organisms, the mono-cellular animals, breathe directly in the medium in which they are placed, just as the tissues breathe in the blood. A strange feature consists in the existence of certain animals, of complex structure, the histological elements of which breathe directly in the air: such are the *insects* and articulated animals in general. In these the exterior air is brought in contact with each histological element by means of a number of small and very minutely ramified tubes (*tracheæ*), so that there is no intermedium between the tissues and the respirable gaseous medium; so in these animals there is no need of a very active circulation of the blood, which is not intended as a medium for respiration, but simply a nutritive fluid in which the tissues are steeped.

The interior phenomenon constituting the respiration of the tissues is *oxidation*, or *combustion*, in short. In regard to this, we must first show in what consists the essential difference between the respiration of the animal and vegetable tissues.

The respiration of the vegetable tissues consists in reduction (at least during the day, and under the influence of the solar light); vegetables absorb carbonic acid, which they reduce, in order, with the addition of water, to form hydrocarbons; by reducing also the water absorbed, they form fatty substances; they also absorb oxidized compositions from sulphur, which they reduce, in order to form the sulphides of allyl, for instance (in garlic); they absorb in like manner the nitrates, which they reduce to form albuminoids. All these phenomena of reduction occasion the evolution of oxygen, and accumulate in the vegetable tissues what are called *forces of tension;* in other words, these tissues *store up the solar heat*, and employ the latter to pro-

duce the reductions which we have mentioned, and again this heat may be transformed into *vis viva*, when the combustion of the vegetable tissues takes place.

This is precisely the office performed by animals, whose tissues consume the elements furnished by the vegetable kingdom, oxidize and decompose them into carbonic acid and water, thus producing heat and force (two synonymous or equivalent words: see p. 78, *mechanical equivalent of heat*). The interior phenomena of nutrition oxidize carbon, hydrogen, and sulphur: nitrogen apparently yields less readily to this organic oxidation, and the urea, which represents the final product of combustion of the albuminoids, contains nitrogen which is in a free state, or at least not combined with oxygen, because the urea is estimated by decomposing it into carbonic acid and nitrogen[1] (by means of Millon's reagent, — Gréhant; see "*Physiology of the kidney*").

2. *The Office of the Blood in Respiration.*—In those animals which are ranked in a higher class than that of the articulata, the blood serves as an intermedium between the tissues and the respirable mediums. It cannot, however, be said that the blood breathes for the tissues; it neither consumes oxygen, nor produces carbonic acid, but is loaded with these gases, simply for the purpose of furnishing the tissues with the former, and carrying the latter to those surfaces by which

[1] "By comparing the general laws of nutrition of vegetables and animals, we find that the phenomena of nutrition are not alike in the two kingdoms, but that they depend upon each other in exact proportion to their dissimilarity." (Wundt, "Physiologie.") The *plant* (the green parts) forms a combustible material which the animal consumes: it operates by way of synthesis, being an apparatus for reduction which rejects the oxygen. The animal takes from the plant, either directly (as the herbivora) or indirectly (as the carnivora), the carbonates and other substances, and consumes these. The animal works by analysis, and is an apparatus for oxidation. By means of this series of metamorphoses matter passes from the inorganic to the vegetable kingdom, and thence back into the animal kingdom, and again returns to the inorganic kingdom: earth and air, plant and animal, earth and air, forms an unbroken chain: such is the rotation of matter. It must not, however, be supposed that there is no exception to this rule, for *reductions* are sometimes observed in animal organisms, as well as *oxidations* in vegetable organisms: neither is there any well-defined boundary existing between the two kingdoms. (See, on this subject, "La Circulation de la Vie," by J. Molesehott, Freneh translation. Paris, 1866.)

it is to be expelled. In the fœtus this intermediary function is twofold: the blood of the fœtus does not make the exchanges directly with the exterior air; it receives oxygen, and gives out carbonic acid, only indirectly, through the blood of the mother; it has, by means of the placenta, one more *station of transit* between the tissues and the exterior air than in the adult life.—The means by which the elements of the blood serve as the vehicle for oxygen and carbonic acid has already been sufficiently indicated in our preceding study (red globules of the blood and their hemato-crystalline; the serum and its salts, see pp. 122 and 130).

The perfect condition of the blood globule, which indicates the capacity of the blood to absorb oxygen, thus has an effect on the phenomena of oxidation; and the products of combustion, therefore, vary in quality, and even in quantity, in a corresponding manner. This Ritter especially sought to decide by studying the *chemical modifications through which the secretions pass when under the influence of agents which augment, annihilate, or modify the capacity of the globule for the absorption of oxygen.* He studied the effect produced by the following compounds: *oxygen, protoxide of nitrogen, oxide of carbon, compounds of antimony and arsenic, phosphorus and the salts of soda, and the acids of the bile.* These substances are divided into two classes, according to their action on the blood globule: the first includes oxygen, the protoxide of nitrogen, and the oxide of carbon. These three agents do not destroy the form of the globule; it is never dissolved under their influence, nor does it form any hemoglobine crystals. The second class, on the other hand, consists of substances which, whether the quantity be large or small, materially alter the shape of the globule, and give rise to the appearance in the blood of the animal of the crystals which are the distinguishing sign of hemoglobine. The composition of the urine is connected with the perfect physiological condition of the blood globule. When any serious change occurs in the blood globule, and especially when the crystals of hemoglobine appear, the urine is found to contain abnormal principles, which are usually the coloring matters of the bile and albumen. Under these circumstances the urine resembles that observed in a fever.[1]

[1] Ritter, "Des Modifications Chimiques que subissent les Sécrétions sous l'Influence de quelques Agents qui modifient les Globules Sanguins." Paris, 1872.

To these researches must be added those of Manasséïn, as to the dimensions of the red globules of the blood under different circumstances. Manasséïn has recognized the fact that the dimensions of the red globules are least, when, from a pathological increase of activity, these globules are in a condition to yield an exaggerated amount of oxygen (as in fever), or in any condition which increases the difficulty of absorption (as when under the influence of carbonic acid and morphine); on the other hand, they increase in size whenever they are brought in contact with any medium which contains a larger amount of oxygen, or are placed under any circumstances which tend to check the loss of oxygen (as when under the influence of refrigerants, quinine, alcohol, hydrocyanic acid).[1]

The blood acting as the vehicle of the oxygen, the more blood an animal possesses, the larger reserve of oxygen it will have in its circulating reservoir, and, consequently, will longer be capable of supporting the privation of air; thus, an animal which has lost a large quantity of blood cannot long exist without constant renewal of oxygen, owing to the fact that, in losing the globules of the blood, it has lost the oxygen which was stored up in them. The power of resistance to suffocation exhibited by some animals has long seemed inexplicable: in the case of the diving animals, however, Paul Bert has shown that this power is simply owing to their possessing a larger quantity of blood: thus a duck possesses one-third, or even one-half more blood than a land fowl of the same weight; if the latter be immersed in water (or strangled), it dies in two or three minutes, while the former will hold out for seven or eight minutes. This power of supporting the privation of air is due to the large quantity of blood possessed by the animal, which forms a sort of *storehouse of oxygen in combination* (P. Bert, *op. cit.*)

3. *Function of the Pulmonary Surface.* — The blood, which may be considered as the intermedium between the tissues and the respirable medium, may be also the seat of gaseous exchanges over the whole surface which comes in contact with this medium. Thus, in the frog, respiration takes place by means of the surface of the skin as well as by the mucous surface of the lungs. If the mesentery of a batrachian be stretched out, and the circulation examined, the contents

[1] See an excellent epitome of Manasséïn's researches, by E. Lauth, in "Gazette Médicale de Strasbourg." 1er août, 1872.

of the mesenteric veins, which were dark colored at the beginning of the operation, are soon observed to become bright red, like arterial blood; this is because oxygenation has been effected simply by the exposure to air, both of the surface of the mesentery, and of the intestine during the experiment; and the frog, thus prepared, breathes (in the pulmonary or respiratory sense of the word) through the lungs, the skin, and the mesentery. In speaking of the epithelium of the lungs, we have already mentioned that oxygenation goes on in the intestinal mucous of the *cobitis fossilis* (water loach). Finally, the skin of the superior animals, and even of man, appears to have some share in the exchanges effected by respiration between the blood and the outer air, especially in respect to exhalation; we shall return to this subject when studying the functions of the cutaneous surface.

These exchanges, however, for the most part, are made on one particular surface, which, in the case of those animals which live in the air, is represented by the lungs.[1] The lungs are the organ of respiration, insomuch as they are the place in which exchange goes on between the blood and the outer air: *respiration* has been hitherto studied from this point of view, but our present knowledge of the subject allows us to regard the *pulmonary function*, not as the only seat of respiration, but as representing a link, and as one of the least important, in the long chain of processes which, beginning in the very depth of the histological elements, terminate in those surfaces which come in contact with the external medium.

The function of the pulmonary surface can thus be fully understood only in the light of the recent acquisitions of physiology; and the *history of respiration* offers a most singular collection of hypotheses formed on this subject by physiologists and physicians: some maintaining that the pulmonary respiration has only a mechanical office, by which

[1] These exchanges take place in the epithelium of the bronchi, as well as in that of the alveoli. The columnar epithelium of the bronchial mucous readily allows the production of hematosis (or pulmonary gaseous exchanges). In order to prove this, we need only remember the anatomical fact that *the bronchial arteries have no corresponding veins*, and that their blood, having nourished the bronchi, becomes *oxidized* by contact with the air, and, consequently, flows immediately into the pulmonary veins, which latter bring it back to the heart with the general mass of the blood that has become *arterial blood*.

the blood passes through the vessels of the lung, owing to the expansion of the latter; while others hold that its function is entirely physical, and consists in *cooling* the blood by contact with the air. This cooling does take place, as we have said, but it is a secondary process, and of scarcely any importance (Cl. Bernard). Only a small proportion of the cold air which enters the respiratory tree at each respiration penetrates as far as the pulmonary lobules, and that only after it has been warmed. The larger part of the air inhaled is confined to the respiratory organs, the nasal chambers, the pharynx, and the large bronchi. Lavoisier was the first to furnish any certain knowledge as to the process of respiration; confirming the ideas entertained by J. Mayow,[1] in regard to his *spritus igno-aereus*. Lavoisier showed that respiration was a process of combustion, but did not, however, determine the exact seat of the combustion: Lagrange, Spallanzani, and William Edwards proved that these oxidations take place in the tissues, and that the lungs are only the place from which the gaseous products of these interior combustions are exhaled.

It is not, however, sufficient to know that the blood in the lungs simply evolves carbonic acid, and imbibes oxygen; the necessary conditions of this interchange must be distinctly stated. First, in regard to the oxygen, we already know that this gas is not dissolved by the blood, but is absorbed by the red globules (Hematocrystalline). Neither is the exhalation of the carbonic acid produced, as might be at first supposed, simply by a *diffusion* of the gas, or by the *evolution of dissolved gas* in an atmosphere containing very little of the gas. The air of the pulmonary vesicles contains actually 8 per cent of CO^2, which is a condition unfavorable to the evolution of the carbonic acid of the blood; while, on the other hand, a portion of the latter is, not dissolved, but combined with the salts of the serum (carbonates and phosphates. Emile Fernet. See p. 129). It is, therefore, probable, that some process takes place in the lungs, the effect of which is to forcibly *expel* the carbonic acid; this process is undoubtedly chemical in its nature, and some experiments seem to show that it somewhat resembles that, by means of which the acids evolve carbonic acid from the carbonates. These facts gave rise to the theory formed by Robin and Verdeil as

[1] See Gavarret, "Les Phénomènes Physiques de la Vie." Paris, 1869.

to the existence of a *pneumic acid* (see p. 128); the existence of this acid has not been confirmed; and, moreover, it has been observed that whenever, in the course of experiments, the oxygen mingles with the venous blood, even *in vitro*, carbonic acid is immediately evolved: this leads us to imagine that the combination of the oxygen and the globule (oxy-hemoglobin, the spectroscopic features of which we have already studied, p. 119), possesses properties similar to those of an acid, and thus occasions the evolution of carbonic acid from the venous blood. The absorption of oxygen is thus doubly important in respiration, both for its own sake, and as the cause of the evolution of the carbonic acid previously formed.

D. *Asphyxia.*

The preceding remarks will enable us to point out, in a few words, the various methods by which *asphyxia* may be produced. Asphyxia may be caused, either by *deprivation of respirable air*, or by *intoxication*, that is to say, by the absorption of any pernicious gas.[1]

a. Asphyxia, caused by *absence of respirable air*, may be produced in two ways, — either by there being no oxygen to be absorbed, — or by the carbonic acid being no longer evolved from the blood.

1. Animals die in an atmosphere which is not constantly renewed by the admission of fresh air, *when they have exhausted the greater portion of the oxygen*, provided that the carbonic acid formed be taken away, in order to avoid the inconvenience produced by its accumulation; reptiles die when all the oxygen is exhausted, the mammifera when only 2 per cent remain; and birds, when there is only 4 or 3 per cent of the quantity left (Paul Bert). These facts explain the feeling of distress experienced by aëronauts and by travellers who ascend high mountains: the diminution of the external pressure produces the same effect as rarefaction of the oxygen; respiration is, consequently, performed with difficulty, and there is a lack of oxygen for the purpose of keeping up combustion, and for producing heat and force; fatigue, chill, and a tendency to sleep, follow. These effects are produced in an exaggerated degree while ascending mountains, because the traveller is then obliged to exert

[1] See "Nouveau Dict. de Méd. et de Chirurgie," Vol. III. art. *Asphyxie*, par P. Bert.

considerable muscular force. These different symptoms, especially the lowering of the temperature, appear, however, to come from another cause, which can only be explained by means of the knowledge recently acquired as to the mechanical equivalent of heat (see p. 79). L. Lortet, who has studied the mountain sickness[1] (*mal des montagnes*), by the aid of almost every registering instrument now employed in physiology (the sphygmograph, the anapnograph, special thermometers, etc.), attributes the cooling of the body to the fact that the internal combustion is unable to maintain the previous temperature, which has to contend at once against the external cold, and the loss of the heat which is being transformed into muscular effort: in short, the intensity of the respiratory combustion increases in proportion to the force expended (Gavarret); heat is transformed into mechanical force, sufficient heat being formed for this purpose, in accordance with the density of the air and the quantity of oxygen inhaled. "In ascending mountains, however, and especially when at a great height, and on declivities, where the labor of ascent is very great, an enormous quantity of heat is required to be transformed into muscular force. *This expense of force consumes more heat than the organism can furnish;* consequently the body grows sensibly colder, rendering frequent halts necessary, for the purpose of recovering warmth. During the process of digestion chill is scarcely perceptible: consequently the guides advise travellers to take food once in every two hours, or thereabouts."

These facts serve to explain the effect produced on the health and pathology of the inhabitants of high mountains, caused by the feeble pressure of the atmosphere in which they live. These men, as has been shown by Jourdanet, exist in an atmosphere containing an insufficient quantity of oxygen: they are *anoxyhematics*.[1]

2. If an animal be shut up in a confined space, and a sufficient quantity of oxygen be admitted, while the carbonic acid produced by respiration is allowed to accumulate, *the animal will die, as soon as the proportion of this gas becomes too great;* the time needed to produce this effect differs greatly

[1] L. Lortet, "Deux Ascensions au Mont-Blanc en 1869, Recherches Physiologiques sur le Mal des Montagnes." Paris, Victor Masson, 1869; and "Revue des Cours Scientifiques." 1869–70.

[1] Jourdanet, "Le Mexique et l'Amérique Tropicale." Paris, 1864.

in different animals. Not that carbonic acid is a *poison*, but only that the excess of this gas (or its too great pressure) in the air, hinders the egress of that which is in the blood; the blood is thus prevented from collecting the gas evolved from the combustion of the tissues, and the respiration of the latter becomes impeded.

In the case of asphyxia in a confined atmosphere, both the causes which we have mentioned are found to exist; diminution of oxygen and increase of carbonic acid. Both occur, but in different and varying proportions. By means of numerous experiments, which we have not space to describe, Paul Bert has reached the conclusion that death in a confined air is caused, in warm-blooded animals, by the want of oxygen, and, in cold-blooded animals, by an excess of carbonic acid.[1]

In a natural death, whatever be the cause, the blood, arterial as well as venous, loses all its oxygen. This is why Paul Bert pronounces the somewhat paradoxical opinion that "death is always owing to asphyxia."

b. The type of *asphyxia by intoxication is asphyxia by carbonic oxide;* this gas constitutes the poisonous agent in cases of asphyxia from the fumes of charcoal (Leblanc). Here, the red globule is first affected; we have already seen, in studying the spectroscopic features of the blood (p. 119), that the carbonic oxide takes the place of oxygen in the hemoglobin, and we can easily understand that this oxycarbonized hemoglobin is no longer fit to keep up the combustion of the tissues;[2] thus in asphyxia, by means of carbonic oxide, the temperature is lowered (Cl. Bernard). We find, in short, that this asphyxia consists in the depriva-

[1] See Paul Bert, "Leçons sur la Respiration." Leçons 27 and 28.

[2] This intoxication is effected with remarkable rapidity. Gréhant's experiments on dogs show that in an animal breathing air containing one-tenth of carbonic oxide, the arterial blood, between the tenth and the twenty-fifth second, contains 4 per cent of carbonic oxide, and only 14 per cent of oxygen; and that, in a space of time varying from one minute and fifteen seconds to one minute and thirty seconds, a large proportion (18.4 per cent) of carbonic oxide appears in the blood, while the quantity of oxygen diminishes until it is reduced to 4 per cent. We may therefore conclude, with Gréhant, that, from the first moment that a man enters an atmosphere which is heavily laden with carbonic oxide, the poison of this gas is absorbed by the arterial blood, or, in other words, almost instantly takes the place of oxygen in the globule, rendering it incapable of absorbing oxygen.

tion of oxygen; this deprivation, however, works by means of another mechanism than that already mentioned; being simply due to the fact that the blood has lost its power of acting as the vehicle of the gas. The carbonic oxide does not exert its poisonous influence directly upon the tissues: Paul Bert has shown that the presence of this gas has no effect upon the gaseous exchanges constituting the elementary respiration of the tissues, when in contact with the oxygen.

Some gases act directly on the anatomical elements as poisonous substances; in such cases *asphyxia*, properly so-called when speaking of *respiration*, does not take place, but a poisoning is produced by a gaseous agent: as, for instance, compounds of cyanogen.

Paul Bert's researches on the subject of the influence of compressed air have led to the discovery of the singular and unlooked-for fact, that if oxygen be sufficiently condensed it becomes poisonous. If an animal (a dog, for instance) be placed in pure oxygen, at an atmospheric pressure of 5 or 6, or, what amounts to the same thing in ordinary air, at a pressure of 20 atmospheres, it exhibits the most alarming symptoms, consisting in attacks of clonic convulsions similar to those produced by strychnine. These effects begin to appear at the moment when the arterial blood of the dog, instead of the normal proportion of 18 to 20 cubic centims. of oxygen to 100 cubic centims., contains only from 28 to 30. If the proportion reaches 35 cubic centims., death usually follows. It is remarkable that the convulsive movements continue after the animal has been placed again in the fresh air, and after the blood has been restored to its normal condition. This seems to show that, under the influence of this remarkable hyper-oxidation of the hemoglobuline, a poisonous product is formed in the blood, the effects of which resemble those produced by strychnine or carbolic acid.[1]

E. *General results of respiration.*

The gaseous interchange in the lungs is thus only the result of the products of the partial respiration (combustion) which takes place in the different departments of the organism: since to breathe is to live and to perform the functions of life, the measure of the life and energy of the working of the organism in general will give the amount of the pulmonary gaseous exchanges. Under different circumstances consider-

[1] Paul Bert, "Comptes-rendus de l'Académie des Sciences." 1872–73.

able variation is observed in the quantity of oxygen absorbed and carbonic acid exhaled; these exchanges have been shown to be in direct proportion to the activity of the organs; they are greater in wakefulness than during sleep; after eating, more oxygen is absorbed, and more carbonic acid exhaled; movement, and muscular labor in general, increase these exchanges to their highest point; intellectual labor, likewise, increases them, as the nerve globules, and the nervous elements in general, consume oxygen like all other elements, especially when they are at work.

The nervous tissue may be said to require the largest quantity of oxygen, that is, of arterial blood; the first symptoms of asphyxia are agitation of the nerves, ringing in the ears, dimness of sight, mental disturbance, and loss of consciousness, all which begin in the cephalic part of the cerebro-spinal system; reflex actions of a medullary nature are also produced (motions resembling those made in self-defence, in flight, and in swimming; also excretion of the fecal matters, the urine, the spermatic fluid, etc.), but these quickly disappear. It seems that, at the moment when asphyxia takes place, the carbonic acid accumulated in the blood acts upon the nervous centres and excites them; thus we find certain physical acts, such as the memory, under these circumstances carried to the highest degree; this occurs in the case of persons apparently drowned, who, on being restored to life, state that at the moment of suffocation the memory reached its highest point: that they saw pass before their eyes in a few seconds, and with astonishing clearness, the whole previous history of their life, many events which they supposed had for ever been banished from thought and memory.[1] This

[1] Brown-Séquard long since drew the attention of physiologists to this *exciting action of carbonic acid* (see "Journal de Physiologic," 1858, and following years). It is principally observed in the muscles (both smooth and striated) which contract strongly in animals killed by strangulation. The movements observed *post mortem*, and the occasional and strange attitudes spontaneously assumed by corpses (particularly of cholera patients) must be ascribed to a similar cause. Cl. Bernard has recently demonstrated that in the case of animals asphyxiated by carbonic acid (strangulation), *the temperature rises while the asphyxia lasts*, and that this increase of temperature occurs chiefly in the muscular system (excited, no doubt, by CO^2), and are produced, as is always the case, by chemical phenomena of combustion, increased by the conditions of the asphyxia which are the cause of convulsions. In this case the muscle entirely consumes the oxygen of the blood, which thus furnishes material for exaggerated phenomena, and,

excitation, produced by an excess of carbonic acid, apparently is chiefly in those nervous centres which govern respiration (and which we shall study shortly: the medulla oblongata, or bulb); the over-excited respiration then becomes hurried, and much more forcible than before, as is observed in cases of dyspnœa. On the other hand, when the blood contains a large quantity of oxygen, the (central) desire to breathe (*besoin de respirer*) is less strongly felt, and respiration ceases or becomes imperceptible: for instance, if artificial respiration be produced in an animal, in such a manner as to accumulate an excess of oxygen in the blood, the desire to breathe is no longer experienced in the nervous centres (the medulla oblongata); these are not, in this case, excited by the carbonic acid, and spontaneous efforts at respiration will almost, if not entirely, cease. Similarly let a man make several rapid and deep inspirations: as the blood is now saturated with oxygen, and contains very little carbonic acid, a certain time will elapse before the desire for respiration is felt; thus divers, after making a number of rapid and deep respirations, can remain for a certain time in the water, without suffering from the complete arrest of respiration.

We see thus that the gaseous exchanges have great influence on the functions of the nervous centres, and especially of the respiratory nervous centre, and that these facts must be taken into account when studying the relation between the nervous system and the production of the mechanical phenomena of respiration.

Returning to the study of the conditions which serve to increase or diminish the respiration of the tissues, or rather, the magnitude of the gaseous exchanges which take place in the lungs, we shall find other differences, depending on constitution, age, and sex: a robust person produces more carbonic acid in a given time than one of a delicate constitution; a child produces more than an adult of the same weight;[1]

consequently, produces calorification (Cl. Bernard, Cours de 1872). This explains *the elevation of temperature observed in corpses* a short time after death (especially in persons who have died of cholera). The fact of this increase was formerly disputed, but it has been proved beyond all doubt, and, now that its mechanism is explained, it no longer appears extraordinary.

[1] This is the case with a child, but not with a new-born infant, nor yet with the fœtus. The combustion which takes place in the tissues of the latter is much less active: thus the muscles of newly born animals consume, in the same space of time, a much smaller quantity of oxygen than those of adult animals of equal weight

this fact is connected with the phenomena of development and increase of active life belonging to the child. One of the most curious of the conditions affecting the quantity of carbonic acid exhaled in respiration, is the influence of sex, and of menstruation in women. The researches of Andral and Gavarret show that the quantity of carbonic acid exhaled by man increases until the age of thirty years, and after that period diminishes. In woman, the quantity of carbon exhaled increases up to the period of puberty, until the appearance of the first catamenial discharge: from this time it remains stationary, until the menopause increases it for a short time, after which it follows the same downward course as in an old man. This is, no doubt, because at each catamenial period a considerable quantity of material flows from the economy with the blood. This material is not subjected to the action of the oxygen, but the products of their imperfect combustion are not eliminated with the gaseous exchanges of respiration; thus, during pregnancy, the menses being suppressed, the quantity of carbon exhaled by the respiratory organs is considerably increased, diminishing as menstruation returns.[1]

The mean result of respiration is as follows: an adult man excretes 850 grms. of carbonic acid (see p. 317) in 24 hours, forming a volume of about 400 litres. A knowledge of this figure is of practical use, inasmuch as it shows how much pure air is required by an adult man of average vigor. A proportion of $\frac{4}{1000}$ of carbonic acid in the air inhaled is admitted to be injurious. Now, if we give out 400 litres of carbonic acid in 24 hours, 16 litres will be got rid of in an hour, which is exactly sufficient to vitiate 4 cubic metres

(the proportion being $\frac{29}{47}$. Paul Bert). By means of this discovery Paul Bert explains the resistance to asphyxia in new-born animals. It is a well-known fact that a dog, just born, may be immersed in tepid water for half an hour, and yet be taken out alive; and it will resist strangulation, or copious bleeding, etc., for a much longer space of time. This circumstance can only be explained by supposing that its circulation still resembles that of its fœtal existence, as the same state of things continues even when the amount of blood has been diminished by long-continued bleeding. The resistance of the newly born animal can be explained only by the fact of a still greater resistance on the part of its anatomical elements, which, consuming less oxygen, can therefore longer support the want of it.

[1] Andral et Gavarret, "Recherches sur la Quantité d'Acide Carbonique exhalé par le Poumon dans l'Espèce Humaine." (Annal. de Chimie et de Physique. 1843.)

($\frac{16}{4000} = \frac{4}{1000}$). We, therefore, require at least 4 cubic metres of pure air each hour we breathe. Taking into account, however, the various combustions and decompositions taking place around us, and which contribute largely to the vitiation of the air, hygienists have doubted the accuracy of this figure, and it is generally admitted that, in order to fulfil all the requirements of hygiene, a man *needs* 10 *metres of pure air every hour.*

V. Influence of the Nervous System on Respiration.

1. *The Respiratory Nervous Centre.* — The mechanical phenomena of respiration (inspiration and expiration) are reflex acts of which the nervous centre is found in the medulla oblongata (bulb), at the level of the gray matter of the fourth ventricle, near the origin of the pneumo-gastric and the spinal nerves. Galen pointed out the importance of this point, and the sudden cessation of respiration (that is to say, of life) which follows injury to the medulla oblongata; but the investigations of Legallois and Flourens[1] have served to decide the position of this *point* or *nœud vital* more exactly.

This centre is situated near those of the motor nerves of the tongue (hypoglossal), of the lips (inferior ganglion of the facial nerve), and of the cardiac fibres of the spinal and the pneumo-gastric nerves. *Labio-glosso-laryngeal paralysis*, which has been so carefully studied by Duchenne (of Boulogne), results from attacks of these centres successively: the tongue is generally affected first; some months later, the muscles of the palate are attacked; then the *orbicularis oris*; followed by an attack of *suffocation* and by syncope.[2]

We have already seen that the blood may directly influence this respiratory centre, according as it abounds in oxygen or in carbonic acid, and, especially, that an excess of carbonic acid coming in contact with the gray matter (in the 4th ventricle) of this nervous centre, increases to the highest degree the *desire to breathe.* The first respiratory movement of the fœtus is, no doubt, caused by the sudden interruption of the placental respiration (see p. 324), producing

[1] See Flourens, "Recherches Expérimentales sur le Système Nerveux." 1842, p. 196.

[2] Duchenne (de Boulogne), "De l'Electrisation Localisée." 1872, p. 564.

in the blood an accumulation of carbonic acid which directly excites the respiratory nervous centre.[1] For the most part, however, respiration is caused by a simple reflex act, of which this gray matter forms the centre; the consideration of which leads us to consider the centripetal and the centrifugal nerves.

2. *The Centripetal Paths.* — The centripetal nerves of respiration are first the *pneumo-gastric*, leading to the medulla oblongata at the *vital point;* to these, however, must be added *the greater number of the sensory nerves of the skin.*

The *pneumo-gastric* nerves transmit to the nervous centre the vague sensory impressions made upon the pulmonary surface, which impressions constitute the desire to breathe. If the pneumo-gastric nerve be cut off above the root of the lung, and its *central extremity* excited, the respiratory movements are seen to become more forcible and rapid, while if the excitation be very great, the contraction of the diaphragm is changed into actual tetanus, so that animals die by arrest of the respiration while in a state of tetanic inspiration. One of the fibres of the pneumo-gastric nerve appears to have a special influence over the respiratory reflex act:[2] this is the upper laryngeal, which appears especially to give rise, in opposition to the pneumo-gastric trunk, to phenomena of *expiration:* if this nerve be cut, and its upper (central) extremity excited, expiration takes place with great force, and if the excitation be very forcible, the animal falls into a state of tetanus of the expiratory muscles. A similar phenomenon takes place in the complaint known as *whooping-cough*, which is only an *affection of the superior laryngeal nerve;* inasmuch as it excites this nerve, and increases the movements of expiration to an extraordinary degree. As, during expiration, the diaphragm is passive, so, when centripetal

[1] It must not, however, be supposed that the carbonic acid alone causes respiration: we know that the elements of the nervous centres consume oxygen, just as do the other elements of the other tissues when at work. The presence of a large quantity of carbonic acid in the blood will produce no respiratory movement if the irritability of the gray matter of the fourth ventricle has ceased, on account of the want of oxygen, as in cases of asphyxia.

[2] Spasm of the diaphragm, so closely associated with intestinal irritation and pleuritis, may be caused by irritation of the pneumo-gastric nerve conveyed to the respiratory centre. I have observed that administration of ipecacuanha tends to the increase of the spasm. (Am. ed.)

excitation of the upper laryngeal nerve takes place, we find it entirely relaxed; and, from this point of view, the superior laryngeal nerve may therefore be considered as a *centripetal moderating nerve of respiration.*

The pneumo-gastric nerve, and superior laryngeal branch, are not, however, the only centripetal respiratory nerves; respiration does not cease entirely when they are cut, although it changes its rhythmical regularity. There are other sensory tracts or paths which bring the respiratory centre into action, and other surfaces than the pulmonary surface which serve as a starting-point to these centripetal nerves. The skin and its nerves perform this office. It is impossible to cut all the nerves of the skin for the purpose of experimenting on these latter centripetal conductors, but the cutaneous surface may at least be preserved from all outward contact, especially from that of the air or of water, this latter medium appearing equally capable with the air of affecting the centripetal nerves of respiration. If the skin be covered with an impermeable coating, such as varnish, the respiration is observed to become more feeble and slower, ceasing entirely in some cases, and in all becoming insufficient: as a sufficient quantity of oxygen is not supplied, combustion is impeded, the animal grows cold, and dies; this method is frequently employed, in physiological laboratories, for the purpose of changing a warm-blooded into a cold-blooded animal by a slow and gradual process of chilling. Some cases of accident have shown that the same thing takes place in man, when nearly the entire skin, or a great part of it, is destroyed. In the large breweries in our towns it happens but too often that a workman falls into one of the immense boilers found in these establishments; even if taken out immediately his skin will be found scorched, and the burns, though sometimes not severe, will be always of great extent, and seriously modify the skin, in its nervous relations; as is always the case in regard to the sensibility of any surface of which the epithelium is injured. In some cases of this kind we have observed that the influence of the *will* is necessary to the performance of respiration with the usual fulness and intensity. The patient then breathes because he desires to breathe, and as the physiological reflex action is insufficient for the purpose on account of the injury to the centripetal organs, the movements of the thorax no longer exhibit their accustomed regularity or apparent spontaneity; if, however, the patient *forgets to breathe*, the movements of the thorax

become slow and feeble, as in the case of an animal whose skin is covered with varnish; the temperature of the body is lowered, and is only kept up by the influence of the will upon respiration. Here it is plain that one of the sources, the *cutaneous source*, if we may so speak, of the respiratory reflex system has been withdrawn, and that the influence of the pneumo-gastric nerve alone is not sufficient to excite the action of the central nervous system. The will supplies this lack of external influence, until the unfortunate patient condemned to this extraordinary species of suffering, at length yields to his fatigue, and falls asleep. Respiration then becomes so feeble that the temperature of the body is considerably lowered, and death finally ensues.[1]

The function of the skin, in regard to respiration, is also demonstrated by a number of medical practices, which are very common, and consist in exciting the respiratory movements by means of irritants applied to the skin: such as friction, effusions of cold water, cauterization, and the more forcible methods sometimes employed to restore life in persons apparently drowned, as well as those employed to excite, in a new-born infant, the first movement of inspiration, which is sometimes delayed and performed with difficulty.

3. *Centrifugal Paths.*—It is scarcely necessary to mention the centrifugal path of the respiratory reflex system here: anatomy sufficiently proves that this is along motor nerves which leave the cervical and dorsal parts of the spinal cord in order to join the muscles of the walls of the thorax; we will only mention, as being the most remarkable, the *phrenic* nerve; this leaves the *cervical plexus*, and innervates the diaphragm; by means of sections of the spinal cord at some

[1] As the pneumo-gastric nerve alone is powerless to excite respiration when the impressions made by the cutaneous nerves are withdrawn, so these nerves are unable of themselves to keep up the reflex action when the pneumo-gastric nerves are cut. The death of animals whose vagi nerves have been divided must, no doubt, be ascribed to this cause. Physiologists have sought to discover in the stomach, in the heart, and the lungs the cause why death so inevitably follows this operation. It has been proved by numerous experiments that the lungs are principally affected; since animals whose two pneumo-gastric nerves have been cut, have been frequently observed to die in a few days, and since the autopsy showed that the lungs were not impaired, death in these cases should be ascribed to the suppression of the sensory or centripetal filaments of the pneumo-gastric nerves. (See Paul Bert, "Leçons sur la Physiologie comparée de la Respiration," p. 496.)

point below the origin of this nerve, all the respiratory muscles may be paralyzed; the diaphragm is thus left to work alone, and, in a case of necessity, it is, of itself, capable of continuing respiration.

II. ANIMAL HEAT.

Our study of the phenomena of the lungs, the respiration of the tissues, and the temperature of the blood, will enable us to examine rapidly the question of animal heat, a question the fundamental data of which we are already familiar with, and which requires, for its completion, only a few special details.

It has long been known that the temperature of the superior animals is, up to a certain point, independent of the surrounding or ambient temperature: these animals are said to have a constant temperature; the mammalia and birds belong to this class. In the other classes of the animal kingdom the temperature of the body depends more or less on the variations in the external temperature; and the animals belonging to these are said to have a *variable temperature.* The former have also, less happily, been called *warm-blooded animals*, and the latter *cold-blooded animals.*[1]

[1] "Between the physiological properties of the muscles and nerves of the warm-blooded and the cold-blooded animals differences exist, which may, perhaps, be owing to the modifying influence of the surrounding or ambient medium. Thus the muscles and nerves of a torpid dormouse, or those of a rabbit under certain circumstances (subjected to gradually increasing cold) which make it resemble a cold-blooded animal, are found exactly similar to those of a frog or a tortoise during the winter. When animals are in a state of torpor, the nervous excitation spreads slowly, and the contraction of the muscles lasts after the excitation of the nerve has ceased, while in those which are not benumbed the contraction of the muscles takes place rapidly at the moment of the excitation, and ceases with it. The special modification produced by cold in the muscles and nerves of animals may, however, be followed by other results. In the warm-blooded animals the nerves and muscles belonging to the system of the great sympathetic nerve, are found endowed with the same properties as the muscles and nerves of the cerebro-spinal system when benumbed. . . . This normal, or physiological, torpor of the muscles and nerves is probably due to a less perfect histological organization, accompanied by a lower degree of excitability or irritability of the organized matter." (Cl.

The temperature of man is constant: a thermometer, placed in the axilla (armpit), shows it to be always about 37° (C.); if we examine the deeper tissues the temperature is found to increase slightly, while in the extremities, which are more exposed, it is somewhat lower.

In order to keep up the temperature of the body and resist the effects of the surrounding atmosphere, the organism, on the one hand, produces heat, and on the other, possesses powerful means of eliminating any excess of heat.

It is now proved beyond all doubt that the combustion which takes place in the organism is the source of animal heat: by means of the oxygen furnished by respiration, we consume the carbon and hydrogen of the food received, or of our own tissues (inanition). It is well known that the calorific capacity of carbon is 8000 units of heat, and that of hydrogen 34,000; in other words, in passing into the state of carbonic acid or of water, 1 kilog. of the former produces a quantity of heat capable of raising 80 kilogrammes of water from 0° (C.) to 100° (C.), while 1 kilog. of the latter will raise 340 kilogrammes.

Man, on an average, develops daily a quantity of heat estimated at 3250 units.

Thus, it is seen that we produce a considerable quantity of heat in 24 hours, and that this quantity increases with increased activity of nutrition, or when the food is more abundant and rich in carbon and hydrogen; the food of the inhabitants of cold countries ought, for this reason, to be richer than that of the inhabitants of the tropical regions, and to contain, especially, a larger proportion of hydro-carbons, without much oxygen, such as the fats which the Laplanders consume in such quantities.

The heat thus produced serves to keep the body at a temperature of 37° (C.), and to raise the fluids, etc., received, to the same temperature. By the aid of a little calculation, joined to what we know of the subject by experiment, we are

Bernard, "De la Physiologie Générale." 1872, p. 249.) Legros observed in the dormouse, during hibernation, phenomena which show still more clearly the close resemblance between the cold-blooded and the hibernating animals. Phenomena of redintegration take place in the latter which never occur during their waking hours. For instance, if the tail of the animal in this state be cut off, it will grow again. (See P. Bert, Recherches Expérimentales pour servir à l'Histoire de la Vitalité propre des Tissus Animaux." 1866.)

enabled to prove satisfactorily that the heat produced by the combustion of the hydrogen and carbon of the food is sufficient to account for all the animal heat; where this heat varies, it is always found that some excess or deficit of combustible material has occurred in the animal economy.

As to the exact region in which these combustions take place, we have seen, in reference to respiration, that their seat is not in the lungs, but in the capillaries, in the very depth of the tissues.[1] We know, besides, that the venous blood is generally the warmest; the contact with the air in the lungs which renders it arterial chills it slightly. The greater the combustion in an organ, the warmer will be the blood that flows from it; as, for instance, the blood of the hepatic veins and the venous blood of a muscle when contracted. All physiologists are now agreed as to the complex nature of the phenomena producing animal heat. The only point upon which they differ in regard to it is the relative importance of the reactions which take place in the blood, and those which have their seat in the tissues. Pasteur, Blondeau, and Camille Saint-Pierre give the supremacy to the former.[2] Bernard recognizes, almost exclusively, not only the importance, but the existence, of the latter. He maintains that heat is engendered in the deepest part of the organs, in close contact with the histological elements, by means of the chemical reactions by which their nutrition

[1] A recent observation by M. Laboulbène seems, at first sight, worthy of notice, in reference to the dispute regarding the seat of respiratory combustion. Being desirous of ascertaining, in cases of thoracentesis, the effect to be produced by taking away the fluid which overflows into the pleural cavity, M. Laboulbène performed this operation, and found that the temperature invariably rises after it. This rise is explained by the changes produced in the state of the respiratory organs by the withdrawal of the fluid. After the operation the lung resumes its functions, in the discharge of which it had been hindered by the compression produced by the overflow of the fluid: the air again freely penetrates the pulmonary vesicles, as is shown by the disappearance of the dulness, and the presence of the respiratory murmur by means of auscultation. This increase of pulmonary activity, however, does not immediately precede the rise in the temperature. The entrance into the lung of a larger quantity of air imparts to the blood (the red globules) a greater proportion of oxygen, and thus enables them to excite the inward processes of nutrition and combustion which take place in the tissues.

[2] See "Moniteur Scientifique," du Dr. Quesneville. Août et novembre, 1872.

and functions are accompanied. These reactions are extremely complex; consisting of separations, fermentations, etc.

The attempt has, however, been made to determine more exactly the seat of these combustions; are they produced in the histological elements themselves, or in the capillary vessels which come in contact with these elements? The German physiologists, who have made a special study of this question, are divided, in regard to it, into two schools. 1. Ludwig and his followers maintain that the act of oxidation and the production of carbonic acid take place in the interior of the capillary vessels. The arguments adduced in favor of this opinion rest chiefly on the recent analyses made by Hammarsten of the *gases of the lymph:* these show that this fluid which carries off the disintegrated parts of the tissues, directly contains a smaller quantity of carbonic acid than the venous blood; whence they conclude that the carbonic acid is not produced in the histological elements. 2. Pflüger considers that the tension of the carbonic acid in the lymph does not give the exact measure of the tension of this gas in the histological elements themselves. In order to estimate this tension as directly as possible, Pflüger has recourse to the normal secretions of the economy (the urine, bile, saliva), which, being the immediate result of the destruction of the cellular elements, must represent exactly the amount of carbonic acid which these contain. In all these secretory products the tension of the carbonic acid is much greater than in the venous blood. Pflüger concludes from this, that carbonic acid is formed in the tissues, and not in the blood, and that the seat of the respiratory combustions is to be found in the deeper tissues.

The heat thus produced in all the different parts of the organism, and more especially in some internal *foci* (the liver) is equally distributed throughout the body by the circulation of the blood; the more vascular any part of the body is, the more active is the circulation in it, and the more nearly it approaches the maximum of its temperature: in some parts (the choroid plexus, articulations, etc.) the vascular richness serves no other purpose than that of warming the part (see *Circulation and Vaso-motors*).

A loss of heat from the surface of the body takes place when the environment is of lower temperature than that of our bodies; the organism, however, possesses various methods of mitigating the injurious effects produced by this

radiation. The entire body is covered by a corneous envelope formed by the superficial layers of the epidermis. The greater part of the body is, moreover, covered with down or hair, enclosing a layer of air, which forms a covering as little adapted to be a conductor of heat as the layers of the epidermis. Finally, a special layer of areolar tissue is found in the dermis (see for all these parts, *Physiology of the external Integument*), called the subcutaneous tissue, or *adipose pannicle*, formed of cells filled with fat, and affording a protecting envelope as regards heat, and appearing most highly developed in cases in which the loss of heat appears most probable (as in that of newly born animals and animals of the polar regions). We also possess numerous and important blood currents, circulating with much greater activity than is required for the purpose of nutrition, in the parts more particularly exposed to cold, such as the pinna of the ear, the face (especially the nose), the hands, and the extremity of the fingers; these currents considerably increase the heat of these parts of the body.

The organism has more difficulty in withstanding a too great rise in the external temperature. For this purpose we find that organs are employed which we have mentioned as being endued with very slight conducting power, such as the cells of the epidermis, the air enclosed in the pilous covering or hair, and the adipose panicle. The most effectual means, however, of resisting too great an elevation of temperature are found in the phenomena of evaporation which take place in the lungs and on the surface of the skin.

With regard to the lungs, we know that, in general, while the 10 cubic metres of air inhaled in 24 hours contain only from 50 to 60 grms. of vapor, the air exhaled contains, on an average, from 300 to 400 grms., and often more: we find, by calculation, that from 200 to 300 heat-units are probably employed in turning this water into vapor at 35° or 36° (C.) (the temperature of the exhaled air); this loss of heat may be carried to a much higher point; for instance, in animals which, like the dog, scarcely perspire at all, except through the lungs, it forms the principal means of equilibrium of the internal heat, when this is increased to too great a degree, as in violent exercise, running, etc.

The evaporation of sweat, from the surface of the skin, is the principal means possessed by man of withstanding an excess of heat. We shall consider this subject at greater length when studying the functions of the skin, especially the

secretion of the *sudoriferous glands;* we need only mention in this place that the function of the exhalation from the skin, alone explains why dry heat is more easily supported than moist: evaporation is almost powerless against the latter, the ambient medium being already almost saturated with vapor; on the other hand, surprising instances have been known of extreme external heat being neutralized by violent sudation, and considerable evaporation of sweat: thus, instances have been known of persons who have supported for ten minutes and more a temperature of 130 degrees (C.). In such cases the secretion of the sweat becomes a hundredfold greater than in the normal state, and, consequently, causes a great loss of heat: the latent heat of the vaporization of water is equal, as we know, to 540.

Man's temperature, at every stage of his life, is connected with the combustion which takes place in the tissues. The temperature of an infant, just born, is nearly the same as our normal temperature; it is only a little lower; a child of this age is, however, very susceptible to outward changes in the atmosphere, and is rarely capable of maintaining the temperature natural to it. Some general laws have been deduced from experiments made on this subject. The temperature of those animals, mammals or birds, which are born with the eyes open, or with down upon their bodies, remains always the same as at birth, provided there are no very decided causes of loss (this being the case particularly in regard to man); on the other hand, birds hatched without feathers, mammals born with the eyes open, and children born prematurely, are unable to maintain this temperature. Thus a rabbit cannot maintain that temperature, 35 or 36 deg. (C.), which it had at birth: the want of activity of combustion is the cause of all young animals offering so little resistance to cold, while it is also the cause of their being able to resist suffocation; their respiration being less active than that of adults, the want of oxygen has less effect upon them than upon persons who require a large quantity for consumption (adults, see p. 334).[1]

As respiration grows more active in man, so the heat produced increases, and the child, a few months after birth, is enabled to support cold in a remarkable manner. Later, the respiration of a young person is superior to that of the adult;

[1] See Gavarret, "De la Chaleur produite par les Etres Vivants." Paris, 1855.

the latter consuming in the proportion of 100, and the former 150.

At the stage where growth ceases, however, a diminution is observed in the production of carbonic acid and the quantity of animal heat; not that the temperature is sensibly lowered, for the greater the size of a body, the less is the loss that takes place by radiation; the cold produced by radiation affects an animal in proportion to its size, the surfaces by which loss occurs varying in individuals of the same kind only by squares, while the bulk varies by cubes; consequently an adult who weighs eight times more than a child, has a surface only four times as large, and loses, proportionately, only half as much heat by radiation (2. — 4. — 8.) This explains the fact that the smaller animals produce more heat (in proportion to their weight and bulk) than the larger animals; the fact being that they lose more by radiation and contact, on account of their surface being larger (in proportion to their bulk).

Aged persons have less animal heat than adults, the phenomena of nutrition and combustion being diminished in their case. There is always a connection between the consumption of oxygen and the production of carbonic acid and of heat (see again, *Physiology of the Muscle*).

Numerous instances of these facts appear in pathology. In cholera, for instance, in which respiration ceases to be a function, properly so-called, and appears to be reduced by the state of the blood to the entrance and exit of the air, the body becomes perfectly cold. In febrile affections there is an increase of caloric, which, we know, is followed by great activity in the circulation and respiration, and in the combustion which takes place in the tissues.

The nervous system has plainly some influence upon the production of animal heat, but this influence is very complicated, and, in some respects, difficult to explain. The heat produced by the organs (muscles, glands, and nervous centres), being in direct proportion to the activity of their functions (that is of the oxidation produced in them), it is plain that the nerves, by means of which they perform their functions, increase the heat by that very fact; thus Haller observed, long since, that a paralyzed limb is usually colder than when in health. Some physiologists have, unfortunately, mistaken the nature of this influence of the nervous system; thus Brodie and Chossat, having removed the encephalon and cut the spinal cord of animals whose respiration they

artificially kept up (a process which induces cooling, if too energetically performed), observed that the temperature was considerably lowered, and thence formed the opinion that calorification is due to a more or less mysterious influence of the nervous system. It has been since discovered that the cerebro-spinal nervous system modifies the production of animal heat by acting on the tissues and giving rise to the chemical processes of oxidation and separation which accompany their vital manifestations.

The effect produced by the *great sympathetic* nerve on calorification is not, however, yet fully decided. We know that if this nerve be divided or paralyzed, hyperæmia of the corresponding parts of the body follows, and is accompanied by a rise in the temperature. On the other hand, galvanization of the peripheral extremity of the great sympathetic nerve causes anæmia of the corresponding parts, accompanied by a fall in the temperature (see p. 170). Are these changes of temperature simply due to a more or less considerable afflux of blood, which forms the vehicle of the heat produced in the principal internal seats of combustion (the liver, the spleen, and the viscera in general), or does the great sympathetic nerve produce any immediate effect upon calorification, beyond the influence exercised by its vaso-motor network? This is a much disputed question, and very difficult to answer. Claude Bernard first directed attention to the subject of the great sympathetic nerve, and its influence on the circulation and on the temperature of the parts through which it passes; and he has lately resumed the investigations which have already yielded such abundant fruits, seeking especially to determine the calorific function of this nerve (course of 1872).[1] This question brings us back to the much controverted subject of the trophic nerves. "Some physiologists have supposed that there exists a third class of nerves (beside the sensory and the motor), called *trophic nerves;* that these immediately govern the phenomena of interior nutrition, and regulate the exchanges which occur in the deep tissues, and which constitute the assimilation and dis-assimilation (constructive and destructive metamorphoses) of the elements. Their existence has never been demonstrated by anatomy, and physiology and pathology have not yet sufficiently proved their necessity" (Cl. Bernard). Claude Bernard, however, seems, after all, to attribute to the great sympathetic nerve some office of this

[1] "Revue des Cours Scientifiques." Mai et juin, 1872.

kind. "We believe that the great sympathetic system is not simply a vaso-motor nerve; it has a direct influence on calorification, its essential office being the regulation of the chemico-physical phenomena which take place in the tissues, when these enter into conflict with the blood by means of the capillary circulation." He holds that this nerve acts as a constant check upon the circulation, and also serves to modify the oxidation that goes on in the tissues as well as the decompositions which produce heat; producing, after section of the sympathetic, an increase of vascularization and calorification, both of which phenomena are entirely local.

III. OF THE LARYNX AND PHONATION.

As we shall presently find that the external integuments are modified in certain parts, for the purpose of more readily receiving the impressions made by the external world, thus constituting *the organs of the senses*, so we shall find that the air-bearing respiratory tube exhibits in the upper part of the neck a special arrangement, constituting the *larynx*, an organ which places man in relation with the outer world, and especially with his kind. This organ is one of the most important of those which serve the purposes of animal life (*fonctions de relation*), forming, as it does, our principal means of communication, in fact, of expression.

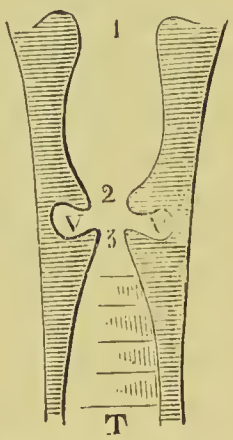


Fig. 84. — Diagram of vertical section of the larynx.*

The other organs of communication and expression are scattered throughout the various external organs: thus the limbs, especially the arms, are organs for expression, the signs of which are generally easily understood. The *muscular system of the face* forms a special organ of expression; all these muscles, with the exception of those of the globe of the eye, are innervated by the facial nerve of the seventh pair, which is under the control of the *medulla oblongata*; thus the thousand varieties of expression presented by the face may be produced by a simple reflex action, without any participation of the will.

* The laryngeal part of the air-passage presents three circumscribed apertures or embrasures: 1, in the aryteno-epiglottidean folds; 2, in the upper vocal cords; 3, in the lower vocal cords. V,V, Ventricles of the larynx. T, Trachea.

Larynx. — The larynx, which is the essential organ of phonation, is only a portion of the *trachea*, modified in its form, and in some degree, in its structure. *In regard to form*, the trachea exhibits, in this part, a contraction, or kind of *strait*, the dimensions of which may be diminished, or increased to such a degree as to bring the trachea almost to its original calibre. This narrowed passage, or laryngeal strait, is multiple, as shown in the diagram (Fig. 84) of the vertical section of the larynx. There are three constrictions, the first of which is circumscribed (from top to bottom); by the *aryteno-epiglottidean folds*, the second, by the false or *superior vocal cords* (which are simply a fold of the mucous), and the third, by the *true vocal cords;* the latter alone forms the veritable *glottis*, or *phonating* aperture. In *regard to structure*, we find the same elements in the glottis as in the trachea, being modified in both to answer a special purpose. Thus, while the epithelium, throughout the whole extent of the respiratory tree, is columnar and vibratile, that which is found at the spur formed by the glottis properly so-called, assumes the pavement form, which is better suited to the functions of the vocal cords. This epithelial coat consists of more numerous layers than the vibratile epithelium, and is also better fitted to prevent the drying of the edges of an orifice through which the current of air passes with so great force. Below the mucous we

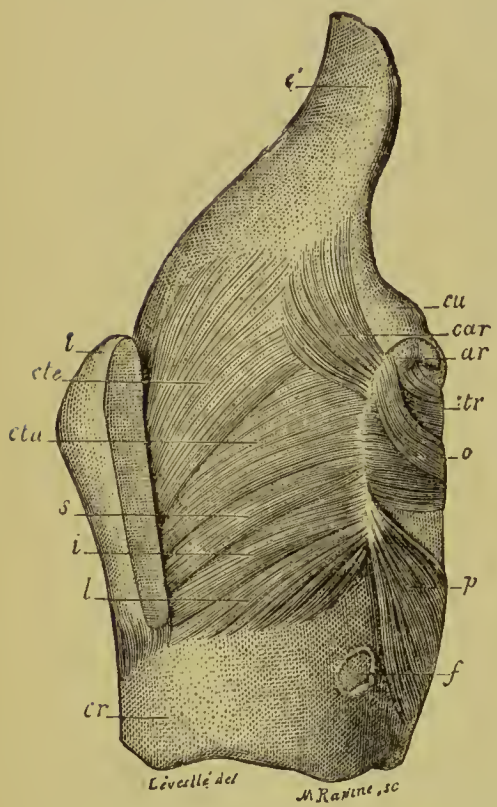


Fig. 85. — Intrinsic muscles of the larynx, seen from the side.*

* The left ala or wing of the thyroid cartilage (*t*) is disarticulated and cut near its projecting angle. *e*, Epiglottis. *cr*, Cricoid. *f*, Thyroid articulating surface. *ar*, Arytenoid cartilage. *tr*, Transverse arytenoid muscle. *o*, Oblique arytenoid muscle. *p*, Posterior crico-arytenoid muscle. *l*, Lateral crico-arytenoid muscle. *i*, Inferior layer, and S, superior layer, of the thyro-arytenoid muscle. *car*, *cta*, and *cte*, Muscular fibres which are not constant, but extremely variable, and are contained in the aryteno-epiglottidean folds, being known by the name of thyro-epiglottidean muscles. (L. Mandl, "Traité des Maladies du Larynx.)

find the elastic tissue which we have already observed along the trachea, formed, as always, of fibres irregularly interlaced and twisted like horse-hair in a mattress; at the glottis this tissue forms a thicker layer, which has been considered in anatomy as a ligament, subjacent to the mucous layer; this is what is called the *vocal cord.*

Below this elastic tissue is also found the muscular layer, as is the case throughout the respiratory tree; in the larynx, however, we find the striated and not the smooth muscle: it forms here, as in all the organs of animal life (*vie de relation*), clearly defined muscular bodies, and with functions well determined (posterior crico-arytenoid muscles, lateral crico-arytenoid muscles, ary-arytenoid, and thyro-arytenoid muscles), (Fig. 85). Finally, the cartilaginous rings of the trachea are also arranged for the purpose of forming special and characteristic pieces or parts (thyroid, cricoid, and arytenoid cartilages), (Figs. 87 and 88).

Aperture of the Glottis.—The inferior laryngeal constriction, or glottis, properly so-called, exhibits, when examined from above, the form of a triangular slit, like the head of a spear, the upper part being in front, and the base behind: this base is formed by the ary-arytenoid muscles. The sides of the triangle are composed in its anterior three-fifths by the vocal cords, in the posterior two-fifths by the edges of the arytenoid cartilages (Figs. 86, 87, 88, 89, 90). These cartilages form triangular pyramids: their base is a triangle, one of the angles of which is anterior, another posterior, and the third external; one of the sides of this triangle is thus internal, and forms the posterior part of the glottis. Each arytenoid cartilage, at its articulation with what is called the *articular facet* of the cricoid (see Figs. 87 and 88, and farther on, Figs. 90 and 91), can turn on its vertical axis, in such a manner that its anterior angle (or *vocal process*) is turned either inwards or outwards, thus necessarily modifying the whole form of the *rima glottidis* (or glottid chink), since this angle is the



Fig. 86. — Aperture of the glottis, seen in the living body by means of the laryngoscope.*

* *or*, Aperture of the glottis. *ri*, Lower vocal cords. *rs*, Upper vocal cords *ar*, Arytenoid cartilage. *rap*, Aryteno-epiglottidean folds. *b*, Cushion on the epiglottis. (L. Mandl.)

point of attachment for the vocal cord, and occupies the anterior three-fifths.

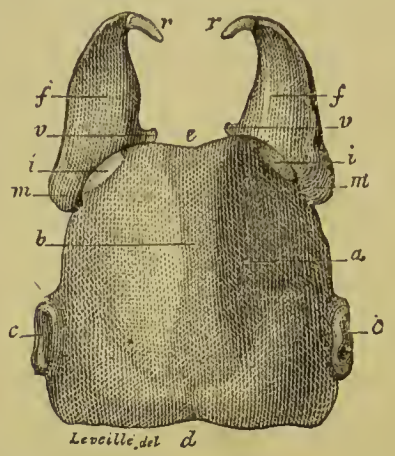


Fig. 87. — External posterior surface of the cricoid and arytenoid cartilages.*

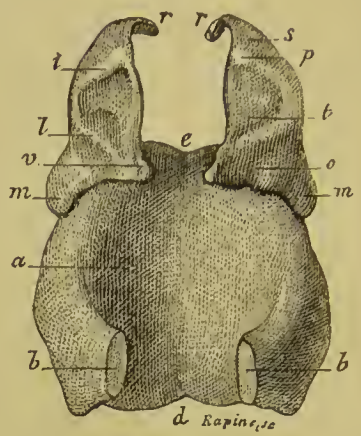


Fig. 88. — Anterior surface of the cricoids and the arytenoids.†

If the anterior angle of the arytenoid cartilage be turned outwards, the glottis will be dilated, and take the *shape of a lozenge* or rhomb (Fig. 89). This effect is produced by the contraction of the posterior crico-arytenoid muscle, which is inserted in the external angle of the arytenoid cartilage, and produces a rocking of the thyroid upon the cricoid cartilage (*mouvement de sonnette*).

If the anterior angle of the arytenoid cartilage be turned inwards, the anterior portion of the glottis takes the form of a slit, which is widened posteriorly into a small inter-arytenoid triangular aperture (Fig. 90).

Finally, this latter opening may be itself reduced to a slit by a second movement which brings the two arytenoids close together (Fig. 91). The first action is produced by the lateral crico-arytenoid muscle, which causes the arytenoid cartilage to swing in a contrary direction to that of the

* *a*, Cricoid cartilage. *b*, Its median projection. *c*, Articulating thyroid surface. *d*, Lower edge. *e*, Upper edge. *f*, Posterior surface of the arytenoid cartilages. *i*, Articulating arytenoid surface of the cryeoid cartilage. *m*, Muscular process (external angle of the base of the arytenoid). *v*, Vocal process, contracted (anterior angle of the base of the arytenoid). *r*, Small cornua. (L. Mandl.)

† Cricoid cartilage, inner surface. *b*, Section of the surface of the annular portion after removal. *d*, Lower edge. *e*, Upper edge of the cricoid. *m*, Muscular process (external angle). *v*, Vocal process (anterior angle). *r*, Small cornua. *i*, *p*, *l*, *t*, , Protuberances and depressions of the antero-external surface of the arytenoid, which serve as points of insertion, being muscular in the case of the most external fibres of the thyro-arytenoid, and ligamentous in that of the upper vocal cords. (L. Mandl.)

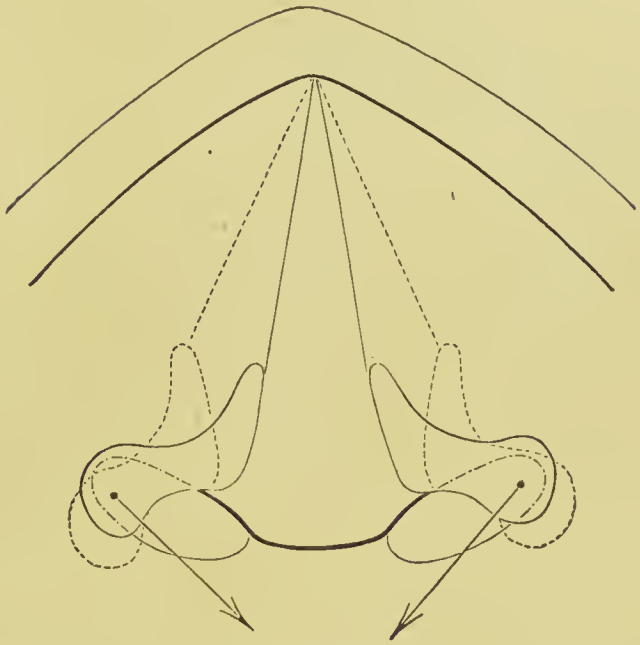


Fig. 89. — Lozenge shape of the glottis, produced by the action of the posterior crico-arytenoid muscles.*

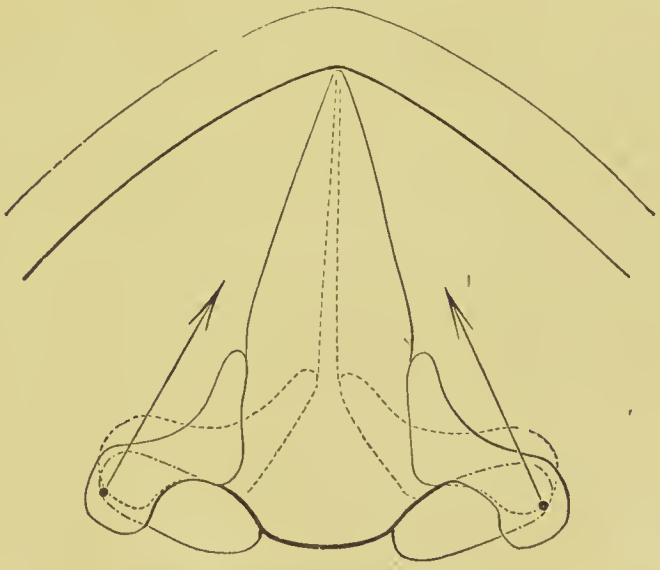


Fig. 90. — Occlusion of the interligamentous part of the glottis.†

* Diagram showing a horizontal section of the cartilages of the larynx, at the level of the base of the arytenoid cartilages. The dotted lines indicate the new position of the cartilages, caused by the action of the muscles working in the direction of the arrow. (L. Mandl, "Traité des Maladies du Larynx.")

† Action of the lateral crico-arytenoid muscles, acting in the direction indicated by the arrows, for the purpose of bringing the arytenoid cartilages and the vocal cords into the position indicated by the dotted lines. (L. Mandl.)

posterior crico-arytenoid; the second action is produced by the contraction of the muscle which forms the base of the triangle of the glottis, the ary-arytenoid muscle, which displaces all the arytenoid cartilages, and makes them slide inwards (Fig. 91).

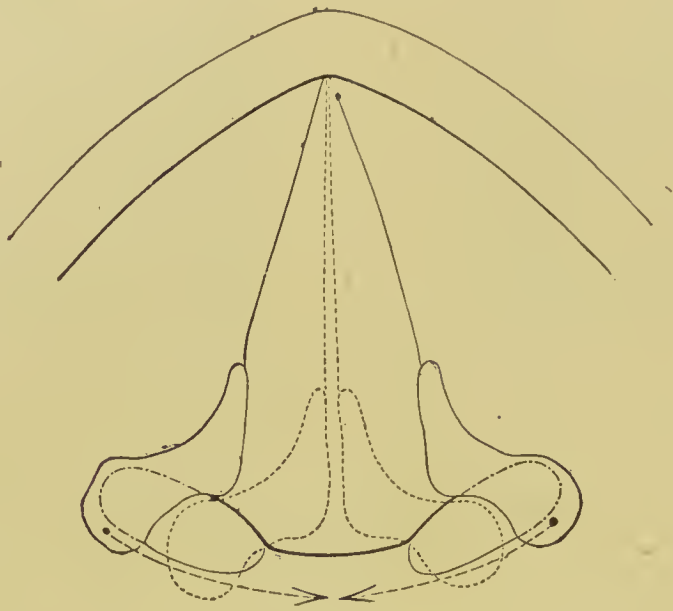


Fig. 91. — Entire obliteration of the aperture of the glottis.*

All modifications in the form of the glottis are owing to these two kinds of movement: the *rocking movement*, and *movement of displacement of the whole box;* the two extreme forms of the glottis thus produced are the lozenge shape, which appears during inspiration, and the linear form, to which a tendency is shown during expiration (see *Respiration*, p. 302): this is, however, more especially connected with phonation and straining: this explains why we often hear a sound, or peculiar cry, uttered by a person who is making any great effort. We also see that one only of the four intrinsic or interior muscles of the larynx serves to dilate the glottis: this is the posterior crico-arytenoid; the lateral crico-arytenoid and the ary-arytenoid serve to obliterate it, and reduce it to the condition of a chink. We must also observe that the contraction of the *thyro-arytenoid* muscle, which is situated in the thickest part of the glottis, like all curved muscles placed around an aperture, completes its

* Action of the arytenoid muscles, median movement of the arytenoid cartilages, in the direction indicated by the two arrows. The dotted lines indicate the new position of the arytenoids and the new form of the glottis. (L. Mandl.)

closure; we shall discover, however, that the contraction of this muscle has to fulfil another and very important function.

We have not mentioned an extrinsic or exterior muscle of the larynx, called the *crico-thyroid.* The influence exerted by it over the glottis is unimportant: it causes the thyroid cartilage to rock forwards, rotating it forwards and downwards on the cricoid cartilage; this action, although it elongates the glottis by elongating the fibrous parts leading from the inner surface of the thyroid to the anterior apophysis of the arytenoid cartilages, has not this effect in phonation, as direct experiment has proved. The functions of this muscle appear to be connected rather with deglutition than with phonation, the muscle itself being innervated by the same nerve as the constrictor muscle of the pharynx (*superior laryngeal* nerve, external branch).

Mechanism of Phonation. — Experiments upon animals, accidental observation in the case of man, and attempts at artificial phonation made with detached larynges, all prove that the sound of the voice is produced in the glottis. In forming this sound, we know that the glottis contracts: thus, it was at first supposed that the vocal organ, in its inner mechanism, resembled a *whistle*, the sound being produced by the vibration of the air in passing through a small orifice, and becoming sharper in proportion to the smallness of the orifice.

It is now proved that it is not the air, but the *edges of the glottis*, which vibrate in this organ; the larynx, therefore, rather resembles a *reed-pipe* than a whistle. There is, however, another analogous organ, which also acts like a reed; this is the *buccal orifice, the lips*, which vibrate as in playing the horn, for instance; it is needless to show the anatomical analogy between the orifice of the mouth and that of the glottis.[1]

In order to vibrate, however, the edges of the glottis must be tense. It was supposed that the vocal cords adjoining the mucous were stretched by the contraction of certain muscles. Müller made the experiment of causing a rapid current of air

[1] "There is no authority for comparing the inferior thyro-arytenoid fold either to cords or ribbons: it is much better to call them simply *inferior folds*, or, if an anatomical name be desired, more expressive of their configuration and function, the *vocal lips*." (L. Mandl, "Traité Pratique des Maladies du Larynx et du Pharynx." Paris, 1872.)

to pass through a larynx, in which he had represented the contraction of the crico-thyroid muscles, by the traction of a weight fastened in front of the thyroid cartilage; he thus obtained a sound by the vibration of the vocal cords, stretched by the rocking movement of the thyroid cartilage.

Nothing, however, proves that this is the case in phonation: if the edges of the glottis were stretched in this manner, the glottis would be necessarily elongated; close examination, however, shows that the glottis is elongated scarcely at all during phonation, and since the tension by rocking of the thyroid cartilage is produced by the crico-thyroid muscle, the latter would then play the chief part in the process of phonation. If the nerve leading to it (the external branch of the upper laryngeal nerve) be cut, its paralysis has hardly any effect on the voice, while section of the inferior laryngeal nerve produces immediate loss of phonation, although this nerve leads only to the intrinsic muscles of the larynx, and not to the crico-thyroid.

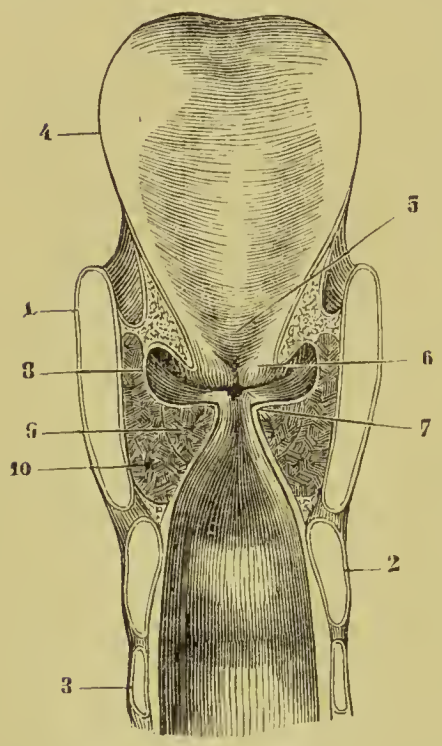


Fig. 92. — Vertical section of the larynx.*

It is plain that the lips of the glottis must be stretched, in order to vibrate, but we do not yet know which of the tissues composing these lips is susceptible of tension, nor what it is which produces this tension.

If we review the three tissues which compose the substance of the lips of the glottis, from the surface to the depth, that is to say, the mucous, the elastic ligament (vocal cord) and the muscle (Fig. 92), and seek to discover which of these three constitutes the vibrating

* This figure plainly shows that the edges of the glottis are essentially formed of muscular tissue. 1, Thyroid cartilage. 2, Cricoid cartilage. 3, First ring of the trachea. 4, Epiglottis. 5, Its median cushion. 6, Upper vocal cords. 7, Lower vocal cords. 8, Morgagni's ventricles. 9, Thyro-arytenoid muscle (the real vocal cord, in a physiological point of view). 10, Lateral crico-arytenoid muscle. (Beaunis and Bouchard, "Anatomie Descriptive.")

body, we shall certainly not fix upon the *mucous*, which forms a protecting envelope, but is not an organ capable of being stretched or of vibrating. The *vocal cord*, although it is called a ligament, does not seem to exhibit the necessary conditions for constituting the vibrating cord, as is generally supposed. This ligament is composed of elastic tissue, that is, of fibres which are not rectilinear, but entangled in every direction, so that, whichever way it is drawn, the tension produced is extremely slight. In the physiological state, however, this tension, which is accompanied by the contraction of the glottis, can only be produced by the crico-thyroid muscle, which, we have seen, plays a very insignificant part in phonation. The *muscular tissue* then remains, viz., the thyro-arytenoid muscle. Now the muscular tissue is very susceptible of tension. What can be more stretched, or more strongly elastic, or what more vibratory than a contracted muscle? The thyro-arytenoid muscle, therefore, in a physiological point of view, constitutes the *true vocal cord*, the only real vibratory element among the tissues which form the lips of the glottis. This vocal cord is stretched, for the purpose of vibration: this is not, however, the effect of any outside influence: it *contracts of itself*.[1] The glottis apparently forms a pipe which vibrates by *contraction* and not by *tension*. As being the source of sound, this organ is unequalled (unique), and cannot be imitated artificially, since we cannot make muscle: the lips (*orbicular muscle* of the buccal orifice) work in a similar manner in the cases previously mentioned.[2]

We shall easily understand the use of the vocal elastic cord, if we consider what would happen if the organ of phonation or voice were composed only of muscle, covered with a mucous surface: at each contraction of the former, the latter would form irregular folds, thus altering the sound of the voice; this happens when the smallest particle of foreign matter, whether mucus or any thing else, is caught in the glottis. An elastic organ is therefore necessary to render the muscle and the mucous independent of each other, by interposing itself between the two. This is precisely the office of

[1] "The contraction of the internal thyro-arytenoid muscle causes the lower folds (lips of the glottis), which were soft and loose during respiration, to be transformed, during the emission of the voice, into an organ-pipe, whose rigidity is in proportion to its tonality. This muscle may therefore be said to be the *accommodating muscle* of the voice." (L. Mandl. 1872.)

[2] See note, p. 353.

the vocal cord, and what we have said of its structure sufficiently proves that it is admirably adapted to this end.[1]

The different degrees of contraction of the glottis have also the effect of increasing or diminishing the production of sounds: as the glottis becomes more contracted the sound becomes sharper, and when it reaches the highest possible pitch, the glottis can contract no more without being entirely obliterated (we are speaking of the *ordinary voice;* there appears to be a special arrangement in regard to what is called the *head-voice*, or *falsetto*).

The anatomical arrangement of the parts obliges the vocal (anatomical) cords to relax as the glottis closes. Yet if these cords formed the vibrating organ, the sounds produced would be lower in proportion to the amount of closure of the lips of the glottis; the narrowness of the aperture, it is true, increases the intensity of the current of air, and may thus help to render the sounds higher; but the whole process is much more simple if we admit that it is the muscle which vibrates: as in contracting, it contributes to the obliteration of the glottis, and even serves to close it entirely; so when it becomes more contracted, or stretched, it can vibrate more readily.

The *elastic cords*, which are called vocal, perform only an accessory part in phonation, that of serving as an intermedium between the mucous membrane and the muscle; they no more prevent the muscle from vibrating than the soft parts surrounding the orbicularis of the lips prevent this muscle from vibrating, as, for instance, when playing on the horn.

The vibrations of the thyro-arytenoid muscle are also assisted by the ventricles of the larynx, whose only office is to give this muscle greater freedom in working (Fig. 92).

Parts connected with the Organs of the Voice.—The sound produced by the glottis is increased by the vibrations of those portions of the air-tube which are above and below the larynx. Special movements, also, take place in these parts, during the production of sounds. Thus, during the emission of

[1] See Henle, "Handbuch der Systematischen Anatomie des Menschen." 1866, Vol. II. p. 259. "The muscular fibres so encroach upon the vocal cords, and are so closely united to the elastic tissue, that we cannot suppose that the elastic fibres vibrate alone, and that the muscular fibres withdraw from the folds of the mucous. . . . The chief utility of the elastic tissue consists in its power of contracting without forming folds and wavy lines, as is the case with some ligaments of the vertebral column."

the higher notes, the larynx rises, the laryngeal muscles being contracted for this purpose and the head thrown back; while, for the lower notes, the larynx descends and the chin is depressed. These are well-known movements, and a patient examined with the laryngoscope is sometimes made to utter high notes, because exploration of the larynx is more readily performed when it is elevated. Attempts have been made to explain these phenomena by comparing them with those produced in wind-instruments. In the first instance, the part under the glottis was supposed to be elongated, and the part above the glottis contracted, and *vice-versâ*, in the second or emission of high notes. This explanation, however, is rendered useless by the fact that the same phenomena are observed when we produce the sound in inspiration; thus, although the physical performance of the organs is reversed, the larynx always rises in the upper notes and falls in the lower.

The elevation of the larynx may be much more satisfactorily explained by considering that the walls of the trachea act as a resonant organ, and that, consequently, in order to heighten a certain sound, they must be in a state of peculiar tension, for the same elastic wall does not vibrate indifferently with all sounds: its tension must be modified in different cases. The higher the note, the more tense the resonant parts are.

The entire nasal system, consisting of the nasal chambers and the frontal, ethmoidal, and maxillary sinuses, is connected with these organs of sound. These cavities are not intended for secretions; but, on account of their coats being formed of somewhat delicate elastic lamellæ, they readily vibrate. Any injury to these organs considerably modifies the tone of the voice. The cartilages of the nose are also resonant organs, as everybody knows that when they are hindered from vibrating the tone of the voice is altered in a peculiar manner.

The vibration of the trachea, the bronchi, the lungs, and the cage of the thorax, also serves to intensify the sounds produced by the larynx. The voice undergoes a change in diseases of the trachea, the bronchi, and the lungs.

The *articulation* of speech, which differs greatly from the simple *cry*, or sound made by the larynx, are almost entirely produced by the working of these sonant parts, and chiefly by modifications in the apertures of the lips and the back part of the throat.

Voice and Speech.—The sound produced at the glottis is only an *inarticulate sound*, differing only in *intensity*, *pitch*, and *tone;* yet this glottid sound, by the re-enforcement of certain of its characteristics at the buccal and nasal cavities, and by the union with other sounds produced at these points, acquires special features constituting the voice and speech properly so-called (see *Organs of the Senses* (*Hearing*) for the explanation of the words *intensity*, *pitch*, *tone*, *sounds*, etc.).

The *intensity* of the sound produced in the glottis depends on the force with which the expiratory current of air strikes the edges of the glottis when so arranged as to emit any decided sound; this intensity depends essentially on the development and the elasticity of the lung, the breadth of the thoracic cage, and the force of the expiratory muscles.

The *pitch* of the sound produced by the vocal lips increases in proportion to their *length* and *tension* (or *contraction*); thus the human voice performs the gamut or scale in passing from the lower notes to the higher; it even forms two series of scales, the lower of which is generally designated under the name of *chest register* (*chest voice*), and the sharper and higher under that of *head register* (*head voice*). These expressions have no meaning in a physiological point of view, since the voice is formed in the glottis in both cases; but what has given rise to them (and, in a certain sense, justifies the use of them) is the sensations experienced during the emission of either the so-called head or chest voice, the accompanying vibrations being more strongly marked in the walls of the chest in the one instance, and in the supra-laryngeal cavities in the other. According to Mandl, the essential modification in the glottis which produces the emission of sounds in the two registers, consists in the fact that, in the case of the chest voice, the orifice of the glottis is open and vibrates throughout its whole extent, while in that of the head voice (or falsetto) the orifice is open and vibrates only in the interligamentous part; the entire intercartilaginous portion is then closed, while the superior vocal cords sink, and are adjusted to the inferior cords, covering a considerable part of them in such a manner as to diminish the extent of the vibrating part (an effect resembling that produced by the tongues employed in the pipes of an organ).[1]

The human voice has, therefore, generally a range of two

[1] See also Ch. Bataille, "Nouvelles Recherches sur la Phonation." Paris, 1861.

octaves, and according to whether these two octaves belong to the upper or lower part of the scale of musical sounds, the human voice has been classified, beginning with the lowest, into the bass voice (from fa to re_3), the barytone (from la to fa_3), the tenor (from do_2 to la_3), the contralto (from mi_2 to do_4), the mezzo-soprano (from sol_2 to mi_4), and the soprano (from si_2 to sol_4), the three latter being women's voices. The differences between them are principally owing to variations in the length of the lips of the glottis; this length is represented in man by the number 25, in woman by 20, and by 15 in eunuchs, their voice being extremely high.

A child's voice is very high, the glottis being smaller than that of the adult. The *change* in the voice takes place at the age of puberty, the development of the larynx causing the voice to become an octave lower in the case of boys, and two notes only in that of girls. In old age, the ossification of the cartilages, and the atrophy of the muscular fibres (?) cause the voice to become still lower, while its intensity is also diminished; thus tenors become barytones (L. Mandl).

The *tone* of the voice is first produced by the lips of the glottis itself. Helmholtz has, we know, demonstrated that the *tone* (see *Organs of the Senses, Hearing*) is due to the fact that the sounds which appear to us so simple are really *composed* of a *fundamental* note, and several accessory notes, called *harmonics* (Sauveur). The varied combination of these harmonic notes, in different instruments, constitutes their special tone. The vocal lips, like the membranous pipes, beside the fundamental vibration of one sound, exhibit partial vibrations which give rise to various harmonics of this note: whence the *different tones of the note produced* by the glottis. What, however, especially marks the tone of the voice, is the manner in which these harmonic notes are reinforced in the cavities and vibrating edges above the glottis (the pharynx, mouth, nasal chambers, etc.), so as to impress their peculiar features upon the voice (see p. 357).

By studying these harmonic notes as being the means by which the tone of the voice is produced, Willis, Wheatstone, Donders, Du Bois-Reymond, and especially Helmholtz,[1] have

[1] See Helmholtz, "Théorie Physiologique de la Musique." Trad. fran. par Guéroult, Paris, 1868.

Laugel, "La Voix, l'Oreille, et la Musique." D'après les travaux de Helmholtz. In "Revue des Deux-Mondes." Mai, 1867.

been enabled to discover the mechanism by which the *vowels* are produced. The vowels are essentially notes produced by the passage of the air through the pharyngeal and buccal cavities; these are arranged in a special manner, and, consequently, resound differently as each vowel is pronounced. When a vowel is pronounced in a whisper, the glottis takes no part in the process, the sound being produced simply by the passage of the air through the supra-glottidal cavities, which at that moment are so arranged as to give utterance to the vowel in question; when the same vowel is pronounced aloud, the supra-glottidal cavities, arranged as before, produce the effect of reinforcing those harmonics existing in the sound made in the glottis, which exactly correspond with those of the vowel to be pronounced. In other words, the buccal and pharyngeal cavities act as sounding boards, which may be variously harmonized.

We cannot carry this analysis any farther here; it belongs to the domain of pure physics, and we will only add that the form assumed by these cavities for the utterance of the different vowels, has been clearly ascertained, and that when the cavities are properly arranged, if the wind from a pair of bellows be made to pass before the mouth, even though the breath be held back, sounds are heard exactly resembling vowels pronounced in a whisper. In general it may be said that "the longitudinal diameter of the *pharyngo-buccal cavity* is reduced, and its transverse diameter increased by the vowel-sounds ah, a, and e (*a*, *e*, *i*); while in pronouncing the vowel-sounds o and u, the longitudinal diameter is increased and the transverse diameter diminished. The movements of the different parts of the cavity follow this general disposition. The lips make a horizontal movement, which is more and more decidedly antero-posterior in the case of the three first vowels, and anterior in that of the two latter. In pronouncing *o* and *u*, the tongue is drawn backward, while in a and e, it is more or less thrown forward. The movements of the *cheeks*, the *velum of the palate*, the *uvula*, and the *pillars* of the fauces, all unite in carrying out this general arrangement, etc. etc." (Mandl, *op. cit.*).

The *consonants*, which form the second element of articulate speech, are not sounds, like the vowels, but rather irregular vibrations, too confusedly mingled to be separately distinguished (see *Hearing*); they are sounds which cannot be distinctly heard by themselves, but differ by the manner in which they begin or finish the utterance of a vowel. The

consonants, therefore, can only be pronounced by being joined with a vowel, whence their name (*cum sonare*). When a vowel is uttered, the cavities of the mouth and pharynx are so arranged as to present certain obstructions to the air which produces the vowel, and the interruption to these latter causes the more or less loud sound of the consonants.

The consonants are *labial*, *lingual*, or *guttural*, according as the obstruction is found in the lips, the tongue, the velum of the palate, or the pharynx; and in accordance with the force employed to overcome the obstruction, whether by a sort of explosion, by vibratory friction, or by a trembling movement, we have *explosive labials* (*b*, *p*), *resonant labials* (*f*, *v*, *m*), *explosive* (*t*, *d*) and *trembling linguals* (*r*), *explosive gutturals* (*k*, *g*), *resonant gutturals* (*j* and *ch*, especially in German), and *trembling gutturals* (the guttural *r*). In some languages, especially the Arabic, the gutturals are very marked, as, for instance, the sound which we designate as *ha*, and which appears to be produced by some obstacle situated as low down as the glottis. It was while seeking to discover the mechanism by which the *really guttural* sounds of the Arab tongue are produced that Czermak invented the laryngoscope which is now so universally employed for the exploration of the larynx.

The labial consonants, especially the explosive labials (*b*, *p*, *m*), are the most easy to pronounce, on account of the simplicity of the movements required: they are the first uttered by children (papa, mamma, etc.), and are those which are most easily taught to certain animals, and are naturally produced in *bleating* (L. Mandl).

This combination of phenomena, by means of which a sound is uttered by the glottis, *modified* by the pharyngeal and buccal cavities in such a manner as to represent a *vowel*, and *joined* to certain *sounds*, produced in the same cavities, and which form consonants, serves to constitute the *articulate voice*, while the intelligent combination of vowels and consonants in *syllables*, and of syllables in *words*, constitutes *speech*. In *spoken words*, the variations in pitch of the syllables are not strongly marked; in singing, on the contrary, the syllables, especially the vowels, which form their essential element, are produced with considerable and harmoniously arranged variations in pitch.

Innervation of the Laryngeal Organ. — The organ of phonation of the larynx is dependent on the inferior laryngeal nerve, which appears to come from the pneumo-gastric,

but really represents the series of fibres which this great nerve trunk borrows from the accessory of Willis, or spinal nerve (internal branch of the spinal nerve). Section of the spinal nerve entirely destroys the voice: this might, therefore, be called the *vocal nerve*. It is remarkable that the other branches of the spinal nerve (the external branch) lead to two superficial and well-known muscles, the sterno-cleido-mastoideus and the trapezius, both which muscles play an important part in expressions by signs, or what may be called the language of the neck and shoulders (shrugging the shoulders, making a sign of negation with the head, etc.). The spinal nerve thus appears to be the nerve of *mimicry* and *phonation*.

While serving for purposes of mimicry, the external branch of the spinal nerve takes an active though indirect part in phonation: this nerve innervates the sterno-mastoideus and trapezius muscles, when, during sonorous expiration, these muscles contract for the purpose of preventing the thoracic cage from sinking suddenly. This peculiarity is easily observed in singers, in whom it constitutes what Manál calls the *vocal struggle;* which consists in a struggle between the spinal nerve and the expiratory movement; Cl. Bernard has demonstrated, by numerous vivisections, that the spinal nerve plays the same part in animals during the utterance of a prolonged cry, and thus has proved that, in a physiological point of view, the spinal nerve is not the *accessory*, but rather the *antagonist* of the pneumo-gastric nerve, since it produces, both in the glottis (by its internal branch) and the walls of the thorax (by its external branch), movements which are opposed to those of respiration.

It is now proved that the nerve centre of phonation is situated in the spinal cord: it is plain that this centre is not found in the brain, for anencephalous patients have been known to scream under the influence of external excitation or internal pain. The centre of *articulate speech*, or rather, the centre of the *memory of words*,[1] appears to reside in the brain; attempts have been made to fix its seat in the anterior lobes, but the observations made on this subject are, so far, contradictory. Both centres are independent of each other, for a cry may be easily uttered when articulation is very difficult. *Amnesia*, or the loss of memory of words, there-

[1] See Aug. Voisin, Art. "Amnésie," in "Nouveau Dict. de Méd. et de Chirur. Prat." Vol. II. p. 53.

fore, must be distinguished from *aphasia*, or the loss of power to pronounce them. The patient suffering from *aphasia* can still write his thoughts, while in *amnesia* he can only express himself by drawing a representation of the objects which he desires.

We will remark, in conclusion, that the working of the organs of the voice, in regard to language, is closely connected with that of hearing; as speech can only come after hearing, a child learns to talk solely by repeating the sounds which he hears every day. A person who has never heard, is unable to speak, and Bonnafont has proved that any one who has heard and spoken up to the age of three, four, or even five years, and then, by any accident, entirely lost his hearing, will gradually lose the power of speech, until, in a few years, he will be scarcely capable of uttering any articulate sounds. We may, therefore, say that a person who is deaf and dumb from his birth is dumb only because he is deaf.[1]

[1] See J. P. Bonnafont, "Traité Théorique et Pratique des Maladies de l'Oreille." 2d edition. Paris, 1873, p. 609.

It must, however, be remarked that persons who are deaf can be taught to articulate words through the medium of sight and mimicry. [Am. ed.]

PART EIGHTH.

EXTERNAL INTEGUMENT.

The Skin.

The skin forms one of the principal surfaces by means of which the organism comes in contact with the ambient mediums: therefore, we shall proceed to study; first its structure, and then its functions in regard to the exchanges which take place, either from within to without, or from without to within; and finally its sensibility, or the power which it has of conveying the impression of the outer world to the origins of the sensory or centripetal nerves.

I. *Structure of the skin — Epidermic productions.*

a. Dermis and Epidermis.—The skin (Fig. 93) is formed of the *dermis* and the *epidermis.* The *dermis* forms a substratum of connective and elastic tissue, serving as a support for the most important part of the cutaneous covering, the epidermis, and contains blood-vessels, nerves, and the glandular organs produced by its deep-seated vegetation. The dermis also contains smooth muscular elements, unequally distributed in different parts: in the skin of the *scrotum* these elements form a continuous layer (dartos). In the nipple, they form a special erectile organ; above all, they are joined to the follicles of the hair, which they can straighten; the contraction of these muscles, under the influence of cold, for instance, produces the sensation known as *having one's flesh creep*, goose-flesh. This sensation, as well as the erection of the nipple, are purely muscular phenomena, and in no way resemble the erection of the erectile vascular tissues: the nipple, for instance, has transverse muscular fibres, the contraction of which increases its length by diminishing its thickness; in the case of the phenomenon of goose-flesh,

the smooth muscles straighten, causing a projection of the pilous bulbs to which they are joined.

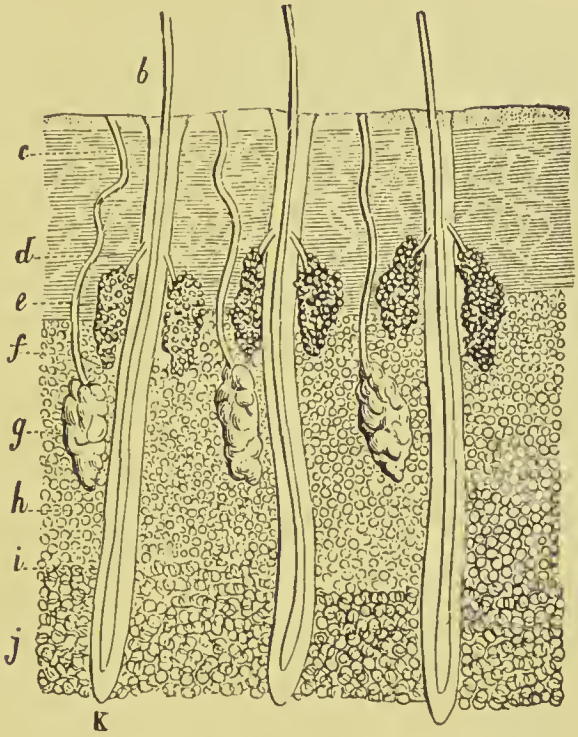


Fig. 93. — Diagram of the skin in general.*

The *epidermis* forms the essential part of the skin: it is this part which first appears in the embryo, at the same time with the epithelium of the digestive tube, the dermis being subsequently formed and organized. This cellular covering is composed of several layers of globules, the deepest being columnar or cylindrical, like those of the intestinal mucous, and constituting what is called the *layer of Malpighi* (or mucous layer, *rete* or *stratum mucosum*); in the more superficial zones, the

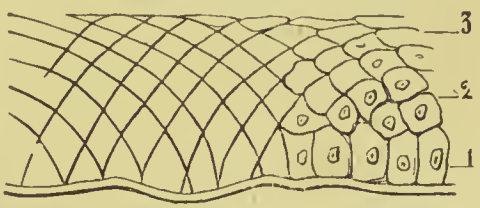


Fig 94. — Diagram of the layers of the epidermis.†

* Section from the scalp (Gurlt). *a*, Epidermis. *b*, Stem of a hair. *c*, *f*, *g*, Sudoriparous gland. *e*, *d*, Sebaceous gland and its excretory tube. *h*, *i*, Adipose tissue. *j*, Bulb of the hair.

† 1, Malpighi's layer. 2, Layer of cells whose dimensions are nearly equal in all directions. 3, Superficial layer of flattened corneous cells, which have lost their nuclei.

form of the cells changes successively, from being polyhedral and nearly of the same dimensions on all sides, and becomes first broader, and finally quite flat, being reduced to a simple band: these successive modifications of form may be tolerably well represented by a series of parabolic lines placed near each other, running in opposite directions, and crossing each other more or less obliquely according to the level of the layers of cells with which their points of intersection correspond (Fig. 94).

b. Life of the globular Elements of the Epidermis.—Beside the change of *form*, an important element of difference between the layers is their change in *structure*, in *composition:* the malpighian layer, and the few layers next to it, are formed of actual globules, that is, albuminous masses of protoplasm, capable of being dissolved into mucus, and are, in short, *living globular elements;* above these layers, however, the structure suddenly changes, and we find only dried-up, shrivelled or flattened cells, which have lost the greater part of their albumen: they are, in short, *corneous cells* (corneous layer), the albumen being oxidized and changed into *keratine.*[1]

Beside these differences in structure and composition between the two parts of the epidermis, we find, as we should expect, quite as marked a difference in their physiological functions. The superficial corneous or horny cells may be considered as no longer living: the globules of the deep layers are essentially alive; that is, they react under the influence of excitants, and actually give rise to inflammatory phenomena: thus, if heavy pressure be long continued, the deep layer is metamorphosed and liquefied, giving out either a simple fluid, containing a few nuclei (blister, *phlyctenæ*), or else purulent matter; cold and extreme heat produce the same effect, as do also some chemical irritants (such as *cantharidine*), known under the general name of vesicants or vesicatories; in this case the middle layer of the epidermis is liquefied, forming a fluid mass which raises the cuticle or corneous layer. If this layer be removed, the serum will flow out, and a white covering be seen spread over the dermis. This is the malpighian layer; and is ready to form again, by its proliferation, the various layers of the normal

[1] Keratine, which is a substance peculiar to the hair, nails, and hoofs, really forms a separate element, being insoluble in potash, unlike other organic substances (Ch. Robin).

epidermis; if, however, the irritating influence be continued, the malpighian layer itself resumes the embryonic globular form, and by its proliferation gives rise to the formation of pus.

This deep and essentially living layer of the epidermis, also gives rise to neoplasms of the tissue, or the different forms of *epithelial* or *cancroid* cancers. In the malpighian layer are found the pigment granules or corpuscles, which shades the color of the skin in the colored races and in some integuments (scrotum, the areola of the nipple, etc.). This pigment of the *rete malpighianum*, appears only after birth. In the negro, however, the edges of the nails, the areola of the nipple, and the genital parts, begin to assume a dark tinge on the third day, and by the fifth or sixth, the black color has spread over the whole surface of the body. The base of the umbilical cord also has a peculiar brownish hue at birth. Researches by Sappey, however, show that the deep layers of the epidermis always contain a small quantity of pigment; the differences of complexion observed between different races are only due to the larger or smaller quantity of this pigment: various influences may heighten its development in the white races; such, for instance, as the prolonged action of heat; in this case the solar rays do not give birth to pigmentary granulations, as a new element, but simply occasion the hypertrophy of those which already exist (Sappey).[1]

The other layers are offshoots from the malpighian layer; its globules multiply constantly, and, by means of this physiological proliferation, the globular elements which have formed a part of the primitive layer, gradually withdraw from the dermis, and form a succession of layers, the oldest of which are always nearest the surface. When these globules extend a certain distance from the dermis, they appear to fall suddenly into decay, and here the line is drawn between the corneous layer and the rest of the epidermis; this sudden death is the fate common to all cells (excepting, perhaps, in such growths as the nails, the globules of which always preserve their nuclei), and, it appears from what we have seen, to the epithelial cells also (intestine). These sudden changes are not surprising, in some cases being much more marked: instances have been known in which the hair, under the in-

[1] See L. H. Farabeuf, "De l'Epiderme et des Epithéliums." Paris, 1873, p. 265.

fluence of some mental shock, has changed its color almost instantaneously; and if this does not indicate the existence of vitality in the elements of the hair, it proves at least that sudden chemical modifications may be produced in them by certain states of the nerves, acting, either directly, or by means of the blood and vessels.

The corneous layers thus produced are destined to be separated from the epidermis, and, consequently, to fall into decay, exactly as we have seen in the epithelium of the intestine. In the present instance, however, the decaying layers do not take the form of mucus, or more or less albuminous flakes, but appear as small scales or pellicles, the remains of dried-up cells. The part of the epidermis nearest to the surface, is formed of these layers of fragmentary detritus, just ready to fall: this is what is called the *furfuraceous* layer, which falls off by slight friction. Pathological causes may sometimes increase this furfuraceous desquamation, and as these epithelial remains contain transformed albumen (keratine), sulphur, iron, etc., in such a case the organism suffers an actual loss; this is the reason that squamous diseases are so dangerous and produce such exhaustion. We have also seen that if the epithelium dissolves into mucus in too large quantities, serious pathological conditions follow, such as *bronchitis*, and *catarrhs* in general. It may therefore be said that what is called a *pityriasis*, or desquamation, in the case of the skin, is a *catarrh* in that of a mucous surface.

We have seen that the desquamation of the epidermis does not generally give rise to a fluid like that from the mucous tissue; there are, however, some less exposed parts of the skin, whose desquamation is less dry, and closely resembles the corresponding product of the mucous tissue; such are the arm-pit, the fatty desquamation of the skin of the gland, and of the inner surface of the prepuce (*smegma præputii*); we shall also find, in the sebaceous glands, saccular recesses of epidermis; as these fall into decay, they become gradually more and more liquid, being finally changed, in the sudoriferous glands, into an extremely thin liquid. The desquamation of the epidermis, in the fœtus, is neither dry nor corneous; it is distinguished by its fatty degeneration (*vernix caseosa*), similar to the smegma præputii; this fatty degeneration continues after birth in certain parts, especially those which are formed last, such as the top of the head, and especially about the median line and the great fontanel, the skin of which appears at birth to be not yet fully matured.

c. *Growths of the Epidermis.* — Besides this desquamative vegetation, the epidermis is also the seat of special growths whose purpose it is to produce more or less permanent organs, such as *hair*, *nails*, *feathers* and other corneous products. The formation of the hair is the type of all the rest: the beginning of this growth is an off-shoot of the epidermis of the *rete malpighianum*, which sinks into the dermis, and here forms a kind of sac, like the finger of a glove, more or less resembling a bottle in shape (*pilous follicle*); at the bottom of this *cul-de-sac*, which grows downwards, a shoot (Fig. 95) of the epidermis is formed, which now growing upwards, towards the surface, lengthens gradually, passes along the follicle (*root* of the hair), and, coming out, forms a more or less decided protuberance outside (stem of the hair: hair, down). These growths are all composed of globular elements similar to those of the corneous layer, being, like this, extremely hygroscopic; this hygroscopy is considerably diminished by means of the fatty matter which the sebaceous glands spread over the skin, and with which they cover the hair as soon as it is developed, these glands, as we shall see, opening into the upper part of the pilous follicles. Some kinds of hair (as the tactile hair of the muzzle of the dog and cat) exhibit on the inside a dermic papilla, which rises to a certain point in the medulla or pith. This papilla is extremely vascular: it therefore would appear probable that it also contains nervous elements constituting it an organ of touch, which has been proved to be the case (J. Dietl, by his experiments on the hair of an ox).[1]

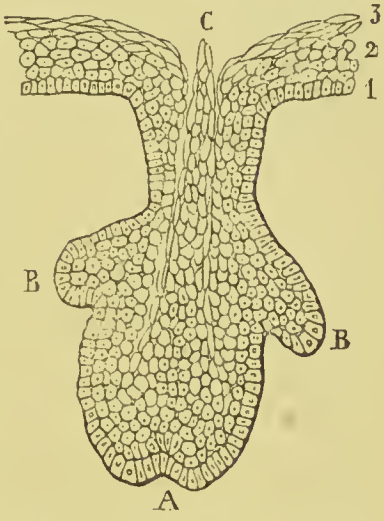


Fig. 95. — Diagram of a deep follicle of the epidermis, or formation of a hair and of sebaceous glands.*

[1] See M. Duval, "Note pour servir à l'Etude de quelques Papilles vasculaires" (papilles des poils). "Journal de l'Anatomie." 1873.

J. Dietl, "Untersuchungen über Tasthaare." (In "Sitzungsberichte der Akademie der Wissenschaften." Wien., 1872, p. 62.)

* A, Bottom of the follicle in which is formed the hair-knob (*bulbe pileux*). B, B, Lateral pouches, origins of the two sebaceous glands. C, Extremity of the young hair, just emerging from its *follicle*. 1, Malpighi's layer. 2, Middle layer of the epidermis. 3, Corneous layer of the epidermis.

II. *Phenomena of exchange effected by the skin.*

These exchanges can be effected either from without inwards (absorption), or from within outwards (secretions).

A. *Absorption.*

Absorption, by means of the cutaneous surface of the skin, is still a much disputed question. One entire system (the iatraliptic or endermic system) of administering medicaments supposes that absorption by the skin does really take place; it must be observed, however, that in such cases the condition of the skin is changed either by mechanical action, such as mercurial friction, or by chemical action, such as the application of alcoholic dyes, rancid pomades, etc. etc. Colin produced absorption by mechanical action in an experiment which is often referred to, and which consisted in causing water impregnated with cyanide of potassium, to drip for five hours upon the back of a horse; the percussion thus produced at length effected the destruction of the sebaceous matter, and caused the cyanide to pass into the system through the skin, and the animal was poisoned by cutaneous absorption.[1] The really physiological question is reduced to whether a healthy skin will absorb water: the ancients maintained that it does, but our present knowledge of the subject seems to show that this is a mistake. Setting aside the many causes which have given rise to this error, it may be proved that no absorption takes place from remaining a long time in a bath: recently, at Vienna, experiments have been made of long-continued immersion, as a new treatment for diseases of the skin, and patients have remained immersed in a bath for weeks and months, without any sensible absorption taking place, the patients continuing to experience thirst, and being obliged to swallow as much liquid as if they had lived entirely in the air. The small quantity which is occasionally absorbed is either introduced by the points of transition between the skin and the mucous, or by the orifices of the sudoriparous and sebaceous glands. It appears to be a general law of animal, as well as vegetable organisms, that the epidermis resists absorption: the vegetable bark, or epidermis of a fruit, closely resembles the bark, or epidermis of an animal; the epidermis of a grape resists the phenomena of

[1] See G. Colin, "Physiologie comparée des Animaux Domestiques." 1873, Vol. II. p. 123.

interchanges, and thus prevents the fruit from drying as long as it is perfect; the slight dryness which appears, is effected by means of the pedicle.

The structure of the epidermis is not, however, well adapted for the penetration of fluids deposited upon its surface, and the question arises how they can pass through these corneous layers covered as they are with fatty matter. Artificial absorption can only be indirectly produced: for this purpose, fatty substances (ointments or pomades) are employed, which mix readily with the fatty matter of the epidermis; if watery fluids are to be introduced, the skin is carefully washed, and cleansed as thoroughly as possible, and yet, in spite of this ablution, scarcely any absorption takes place. That fatty bodies do not allow of the absorption of medicines is due to the fact that these mingle with the oily secretion of the skin; whilst the glyceroles or glycerides (such as plasma, etc.), moreover, are, perhaps, even less absorbable than water. That the skin has any power of absorption must therefore be almost totally denied.[1] If a substance is to penetrate the organism through the skin, it must be placed in the deep layers of the epidermis, the layer of Malpighi, and there is no need to go beyond this; for instance, in vaccination, the substance (vaccinal lymph) need only be placed in contact with those globular layers which are extremely sensitive and impressible: this method is now very generally employed, and is called the *endermic* method, though it might, in some cases, be better called the *enepidermic*.

The skin is permeable by gas: Bichat's experiment is well known, showing that the cutaneous surface of a limb, if immersed in putrid gases, absorbs them; so that, being introduced into the organism, they finally pass out through the lower part of the digestive tube. All kinds of miasma appear to penetrate the organism in this way with the greatest ease. The ready absorption of gas by the skin has led some authors

[1] And yet there are experiments recorded in many standard works, which have been collated and criticised by Dr. Stillé ("Therapeutics and Mat. Med.," 4th ed., pp. 61 *et seq.*), according to which it must certainly be admitted that certain salts in aqueous solutions, as even, perhaps, water itself, can be absorbed by the cuticular covering. Certain experiments undertaken by the Am. editor induce him to believe that bromide of potassium can be absorbed by the endermic method. (*Vide* "Bromides of Potassium," by E. H. Clarke and R. Amory. Boston, 1872.) [Am. ed.]

to imagine that cutaneous absorption takes place only in the case of volatile matters. Rabuteau tells us that if iodine is found in the urine after rubbing with an ointment containing an iodide, or after wearing a shirt dipped in iodide of potassium, it is because the acids of the fats, which at length turn rancid, as well as the acids of the perspiration, have set free the iodine, which, from its volatility, is absorbed by the skin.

B. *Secretions.*

On the other hand, the skin is exceedingly well adapted for the purpose of *secretion*, being the seat of continual growth and decay on the part of the globules; these processes constitute the mechanism of secretion. The furfuraceous desquamation may be considered as a diffuse secretion; the phenomenon of secretion, however, may be still more clearly observed in the *sudoriferous* and the *sebaceous glands*, of whose action the *mammary secretion* is an exaggerated form of result.

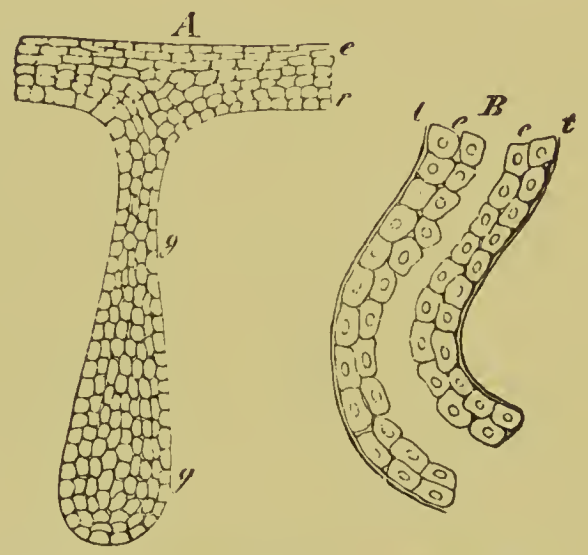


Fig. 96. — Development of the sudoriferous glands.*

The secretory organs are formed in the ordinary manner from the globular elements of the malpighian layer (Fig. 96). This vegetation sometimes appears in the form of a tube,

* A, Development of the sudoriferous glands, in consequence of the proliferation inwards of cells of Malpighi's layer. *e*, Epidermis. *r*, Layer of Malpighi. *g*, *g*, Solid prolongations representing the beginning of the gland (Kölliker). B, Portion of developed sudoriferous canal. *t*, *t*, Tunica propria. *e*, *e*, Epithelial layer.

which sinks to a great depth, and passes through the dermis; then, on reaching the adipose panicle, being unable to go farther, winds round itself, and continues to grow until it forms a glomerulus; this is the coil of the *sudoriferous* or *sweat gland* (see Fig. 98). At other times they form larger but less profound growths, terminating in short, rounded culs-de-sac: these are the sebaceous glands; a vegetation resembling this, but on a much larger scale, produces the secretory elements of the mammary gland (Fig. 99 and 100).

1. *Sudoriferous or Sweat Glands and Perspiration.*—The sweat glands are very numerous: it has been estimated that no fewer than from *two to three millions* of them are spread over the surface of the body.[1] They are found almost everywhere, the greater number being in the folds of the cutaneous surface: in the armpit they form a sort of reddish continuous layer; they are not found on the inner surface of the pinna of the ear, while in the external auditory canal they form a circle of large glands placed close together (*ceruminous glands*).

The tube which forms these glands has about the diameter of a very fine hair: it is at first rolled up (*glomerulus*) in the depth of the dermis; then, becoming straight again, passes through the dermis and continues as a tube, a simple intercellular lacuna, which passes like a corkscrew through the epidermis (Figs. 97 and 98). The average total length of one of these tubes is two millimetres; if, therefore, all the sudoriferous tubes were placed end to end, their total length would be four kilometres: the total mass of the sudoriferous system has, therefore, been estimated at half that of the kidney, or a quarter of the whole renal system; these figures serve to show the relative importance of these two classes of secretory glands.

The fluid secreted by the sudoriferous glands has never been collected in a perfectly pure state, because, in spreading over the epidermis it mingles with other products of this

[1] Sappey counted nearly 120 orifices of sudoriferous glands in a square centimetre in parts of the body where the epidermis is thin. They are still more numerous (nearly 300 to a square centimetre) in the plantar and palmar regions. Their total number, according to these calculations, must reach *two millions:* "it even exceeds this number, although, in making this estimate, we have not taken into account the glands of the arm-pit, which are still more numerous than those of the hand or the foot, and occupy a circulating surface of only three or four cm. in diameter" (Sappey).

organ. It is also very difficult to estimate the quantity of perspiration, especially as it varies greatly under different circumstances: in some cases, as much as from 1 to 100 times. The average quantity of perspiration in 24 hours has, however, been estimated at 1 kil. 300 grams., containing from 15 to 20 grams. of solid matter. If the quantity of perspiration is greatly increased the solid excreta increase also, which explains the weakness accompanying long-continued perspi-

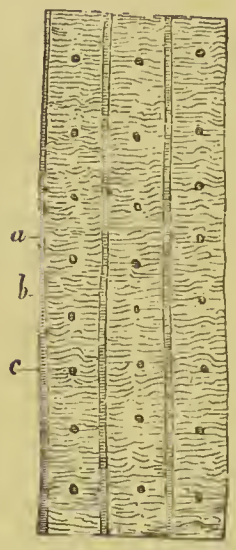


Fig. 97. — Orifices in the sudoriparous glands.*

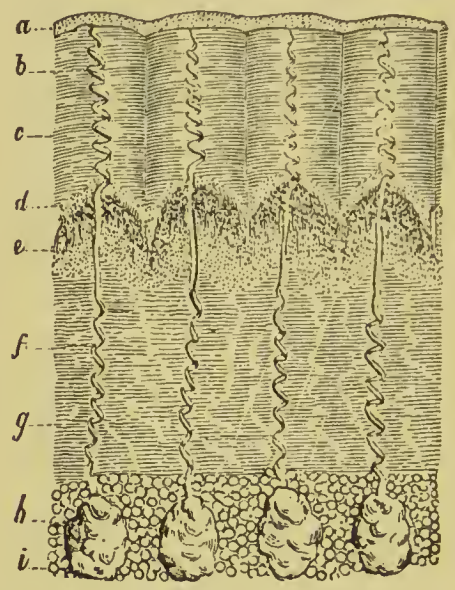


Fig. 98. — Vertical section of the skin, whose surface is represented in the preceding figure.†

ration. The normal and solid product of the sweat (15 to 20 grms.) represents about one quarter of the solid product of urine (60 to 70 grms.); this relation is precisely the same as that which we pointed out between the extent of the two apparatus; it may be generally asserted, that the solid portion of glandular products is in proportion to the extent or mass of the glands, and that it is only the amount of water which is variable.

The *perspiration* or *sweat* is composed of water, the ordinary salts of the blood, fatty principles, and a large number of acids, such as formic, butyric, and propionic acid, as well

* Skin of the hand, palmar region. Skin seen from the upper surface. *a*, Elevation formed by a series of papillæ. *b*, Interpapillary fissures. *c*, Sudoriparous pores. (Gurlt.)

† *a*, Superficial layer of the epidermis. *c*, Middle layer. *d*, Malpighian layer. *e*, Papilla. *f*, Dermis. *h*, Adipose tissue. *i*, Sudoriparous glands, with their excretory tubes twisted in a spiral shape at *b* and *g*. (Gurlt.)

as an acid which is peculiar to it, and is called *sudoric acid* (Favre). The reaction of the sweat is, therefore, generally acid, and becomes still more so when the fatty substances which it contains are decomposed, and allow their acids to be set free. It is these fatty and volatile acids which impart to the blood its acid odor, which differs greatly in different persons, and also in different races of men. The sweat always contains a small quantity of fat; thus there are no sebaceous glands in the palm of the hand, but numerous sudoriferous glands, the product of which always contains a certain proportion of fatty matter. The perspiration of some parts (*the glands of the arm-pit*, and especially *the ceruminous glands*) contains a much larger proportion of fats. Finally, some nitrogenous matters, urea, among others, are found in the perspiration; if the decomposition of these products exceeds that of the fats, ammonia is produced, and the perspiration becomes alkaline. The elimination of the urea, and, in general, that of the products of combustion of the albuminoids is of sufficient importance to render the skin an emunctory similar to the kidney, and which may supply its place in some cases. We shall find that, in the normal state, two-thirds of the nitrogen introduced into the organism is eliminated by the urine; the other third probably escapes, partly by the lung, with the fecal matters, or through the skin.

The sudoriferous secretion was formerly supposed to be only the evaporation of the fluid parts of the blood while passing through the epidermis. The discovery of the sweat glands has shown where this secretion is produced: in order to understand the interior mechanism of the secretion of these glands, the ceruminous glands must first be studied; we find that their thick and fatty product, *cerumen*, is produced by the *imperfect melting* of the globules of the gland; the perspiration of the armpit also is remarkable for the proportion of solid matter, evidently arising from vegetation and decay of the epithelium. We are thus led to believe that the secretion of ordinary perspiration takes place in the same manner, only by means of a far more *perfect melting*, and borrowing a much larger quantity of water from the blood; thus, when the blood is unable to furnish a sufficient supply of water, as in cholera, in which disease the water becomes extremely thick, the perspiration itself becomes viscous, and is known as the *sticky sweat* of cholera patients.

This cellular moulting, or secretion, is chiefly produced by

the influence of the nervous system, which not only acts on the vessels of the skin, but also directly on the glandular elements; hyperæmia of the skin (as occasioned by extreme heat), or great tension of the blood (such as is caused by the absorption of a large quantity of water), no doubt serve to increase the quantity of sweat, but the nervous system produces reflex secretions which are quite as energetic, and have no resemblance to the congestion of the blood-vessels in the skin; if the blood does not furnish sufficient water for secretion, a gland borrows its fluids from the neighboring tissues, exactly as we have seen done by the salivary glands. The profuse perspiration of death takes place when the skin is cold and pale; the common saying that certain emotions produce cold sweats is perfectly correct. Indeed, the "nervous" condition has the chief influence on sudation; we perspire often when some idea, such as fear, presents itself to our minds. These sweats are often confined to some particular part of the body, varying in different persons; some very decided reflex actions produce abundant perspiration round the waist, or in some part of the face; in cases of hemiplegia the sweat appears only on one side of the body; if some drops of vinegar be placed upon the tongue and the mucous tissue of the mouth, large drops of perspiration will appear on the forehead, or sometimes on one side of the forehead, or of the face. The nervous organs for these reflex actions are not yet perfectly known; their centre appears to be found in the spinal cord.

The sweat thus secreted by the sudoriferous coil, follows the excretory tube, until it reaches the epidermis, the different layers of which it traverses by means of a tube without any proper walls, which is a hollow in the midst of these layers. As the malpighian layer contains a large quantity of fluid, and the corneous layer, properly so-called, is very coherent, these layers derive nothing from the perspiration; but the most superficial layer, the pulverulent furfuraceous or porous corneous layer, collects a large quantity in its interstices. The perspiration, as it reaches this point, resembles a river lost in the sands; nearly all the fluid disappears. Thus if the skin of a man in good health be touched, it is found to be slightly damp, and produces an indefinable sensation, which is lacking during that period of a fever in which the perspiration is entirely suppressed. It is only in cases where the perspiration is extremely plentiful that it overflows, after being diffused through the pulverulent layer, and

appears in small drops in the excretory tubes. In general, however, the perspiration remains in the furfuraceous layers, and thus gives rise to the *moisture* of the skin.

This humid condition of a superficial porous layer places the skin and the entire organism in a peculiar state: the loss of heat, which is in exact proportion to the abundance of the perspiration, produces constant evaporation. The human body resembles, in this respect, those porous vases, or *alcazaras*, which are used to cool water by means of the evaporation which takes place on their surface: as sudation is generally increased by the elevation of the external temperature, or by any exertion (muscular labor) which has a tendency to produce heat in the body, we possess a means of defence against any too great accumulation of caloric; we have seen, indeed, in our study of animal heat, that our temperature cannot, without danger, go beyond 40 or 43 degrees (C.) (see p. 343). While, however, the perspiration forms a valuable aid in resisting heat, it also renders us liable to a great danger, as any excess or derangement is followed by a *chill.*

When such a chill takes place, the secretion of the perspiration ceases suddenly; this, however, usually happens too late, and the harm is done: these chills produce extremely serious and varied effects on all the parts of the organism. In olden times the arrest of sudation was looked upon as the most important part of the whole process, and perspiration was looked upon chiefly as an emunctory; its suppression was considered the retention of poisonous materials. The perspiration, no doubt, contains *excreta*, but not, it would seem, in sufficient quantity to produce blood poisoning, and while we consider the cooling effect as the principal physiological office of the perspiration, we look upon any exaggeration of it as the chief cause of some derangements in which the suppression of the perspiration is only a concomitant phenomenon. One of the first effects that follow this cooling is invariably a change in the blood, the fibrine of which increases; this may perhaps be owing to some derangement in the condition of the deep layers of the epidermis, as, indeed, in such cases, ganglionic swellings are often observed, the suffering or agony of the epidermis being, as it were, transmitted to them by means of the lymphatic vessels. Dr. Lang (of Göttingen), however, by studying the effects produced from suppression of cutaneous perspiration, has obtained the following results: on making the autopsy of animals

which have died after being coated with a varnish, he found peculiar crystals of ammonio-magnesia phosphate in the cellular tissue, the peritoneum, and the muscles. Study of experiments of this kind seems to show that when the cutaneous excretion is suppressed, the eliminated products have a tendency to pass through the kidney; this organ is consequently in a state of hyperæmia; later, an exudation takes place in the uriniferous canaliculi, which are finally obliterated; this produces retention of the urea with all the consequences which belong to it. We therefore naturally suppose that this substance being retained in the blood, when decomposed, produces ammonia; this, combining with the phosphates, gives rise to the formation of the above-mentioned crystals of ammonia-magnesia phosphate. Researches made as to cause of death in consequence of burns of a large extent of surface yield the same results. The cause of death, following the suppression of cutaneous perspiration, is therefore hyperæmia of the kidneys, followed by parenchymatous exudation in the canaliculi of the kidney, which are at length obliterated, thus causing retention of the excrementitial substances of the urine.[1]

2. *Glands and sebaceous Secretions.* — The sebaceous glands are found in almost every part of the integuments: they are generally joined to the hair (see Fig. 93), as we have already said, but in parts where there is no hair, they are sometimes found alone, as on the *glans* and the inner surface of the prepuce; finally, certain portions of the integument, such as the palm of the hand, have neither hair nor sebaceous glands (having only sudoriferous glands). The sebaceous glands form, round the hair, numerous culs-de-sac, which may be looked upon as off-shoots of the pilous follicle (Fig. 93 and 95), and surround the neck of the hair sometimes in such numbers as to completely hide the pilous apparatus. These glands form the most simple type of clustered or racemose glands: their contents consist of epidermal globules, the outer ones being well-shaped and exactly similar to the elements of the layer of Malpighi; as these globules, however, approach the centre of the glandular cavity, they become infiltered with fat, hypertrophied, and, finally, separate and allow their contents to escape to form a sort of emulsion of fat and albuminous substances, which fills the cavity of the gland, and is thrown off; the secretion of the sebaceous

[1] See "Gaz. Médic. de Strasbourg." Février, 1873.

glands forms in this way the most simple type of moulting of the globules.

Two-thirds of the *sebaceous* matter thus produced consists of water, — the rest being chiefly fats, some extractive and albuminous substances, and some earthy salts. The fatty substances are the most important in a physiological point of view. It is owing to these latter that the sebaceous matter possesses the property of imparting a certain quantity of grease to the hair, and of imparting an oily feeling to the whole surface of the epidermis, thus increasing its impermeability. Whatever may be the varieties in form and arrangement of the sebaceous glands, their use is always the same; the purpose of the meibomian glands, which are elongated sebaceous glands situated in the eyelids, is to anoint their free edge, and thus prevent the product of the lachrymal gland from overflowing on to the cheeks.

We have already seen that the *tonsil* (see p. 230) may be described as a complex sebaceous organ, developed from a mucous gland, and connected, at its base, with the lymphoid follicles: this tonsil likewise produces a sebaceous matter the use of which is not fully known.

It frequently happens that the secretory globules of the sebaceous glands do not attain their maturity in a regular manner; being imperfectly dissolved, the sebaceous matter remains in the state of desquamated epithelium, instead of becoming an oil or half-liquid fat; it no longer flows easily, and its accumulation in and dilatation of the glandular sac produces sebaceous cysts or *wens*, which grow sometimes to an enormous size. Large quantities of fatty substances are found in these cavities, as well as a surprising proportion of crystallized cholesterine. (In a cyst of this sort, containing 2 kilos. of sebaceous matter, 15 grms. of cholesterine were found.)

3. *Breasts and Milk.* — The mammary gland (Fig. 99) consists of a union of from 15 to 20 highly developed sebaceous glands; the glands of the scrotum and of the fold of the groin sometimes furnish a product closely resembling milk; in the *areola of the nipple* are found immense sebaceous glands, called *erratic lacteal glands*, which exactly follow the variations in development of the mammary gland, going through the processes of atrophy and hypertrophy in the same manner.

The numerous *culs-de-sac* of the sebaceous glands, which culminate in lacteal glands, unite to form the 15 or 20 tubes leading upwards to the nipple, where they open into as many

separate orifices. The structure of this apparatus is similar to that of glands in general: the glandular culs-de-sac are filled with cells resembling those of the sebaceous glands; the epithelial covering of the lactiferous *canals* or *tubes* has, however, a tendency to become columnar. In passing through the nipple, these tubes traverse a sub-cutaneous connective tissue abounding in smooth muscular elements, either transverse or circular; the contraction of these muscular fibres, which are only an exaggeration of the smooth muscles normally attached to the dermis, causes the elongation and stiffness, or, in short, the *erection* of the nipple (see p. 364).

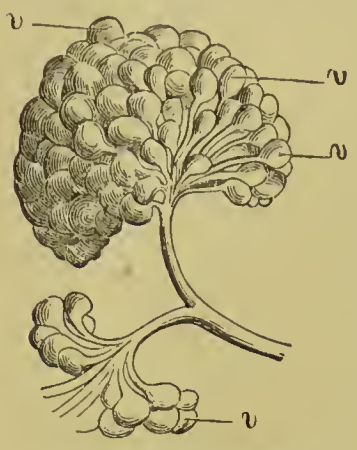


Fig. 99. — Lobule of the mammary gland.*

The *secretion of milk* is effected in the same manner as that of the sebaceous glands: by a moulting of the globules; at the beginning of the secretion, this mode of production may be readily observed, globules being still found which, after undergoing fatty degeneration, are not entirely dissolved, and appear as cells containing numerous drops of fat: these are the globules of the *colostrum* (Fig. 100). The colostrum is thus the result of a secretion not yet firmly established, or rather interrupted by some intercurrent cause, such as the return of the catamenia or pregnancy in a nursing mother.[1]

[1] This opinion as to the formation of milk by the moulting of the cells is not held by all physiologists. Cl. Bernard's theory is as follows: "There takes place a sort of budding (*bourgeonnement*) of the superposed cells, in which the materials of the milk, casein, butter, etc., are prepared; the coat of the lacteal cell is then dissolved in an alkaline fluid, and milk is produced." Ch. Robin, on the contrary, maintains that the *culs-de-sac* of the breast, which are lined with epithelium during pregnancy, and while little or no secretion is taking place, lose this epithelium as soon as the secretion is established. If this be so, the special phenomena of secretion must take place in the wall proper of the *culs-de-sac*. Ch. Robin also explains the origin of the *globules of the colostrum* by looking upon them as white globules, degenerated or transformed leucocytes. Whenever the leucocytes (white globules) remain

* *v, v, v,* Glandular vesicles, forming by their union a lobule.

When secretion has actually begun, the moulting of the globules is complete, and it is difficult to find in the milk any trace of its cellular origin. The quantity secreted varies, but may be generally estimated at 1.300 litre in 24 hours: the quantity of bile produced is about the same, but the milk contains more solid elements than this latter fluid, the proportion being 12 parts in 100 (while it is only 5 parts in 100 in the



Fig. 100.—Mammary gland during lactation. Milk.*

bile). These 12 parts are composed nearly in the following manner, at least in the case of women: first, 1.5 grm. *of various salts* (in 100 grms. of milk), being for the most part salts of the blood, and especially phosphates of lime and potash (a little soda), and a certain quantity of iron;—2 grms. of *fat* or *butter* (margarine, oleine, etc.); this fat is the only physical element in good milk, and appears under the form of small drops of various size, which impart its peculiar white appearance to the milk (emulsion)—3 grms. (in 100 grms. of milk) of *caseine*, an albuminoid substance, which is coagulable, not by heat, but by the gastric juice, or by pepsine, as we saw when studying digestion. The principal element (in woman's milk) is, finally, the *sugar of milk*, which is in the proportion of 4 parts in 100, or a little more.

motionless for a considerable time, they pass into a granular state, becoming three or four times larger than when in their normal condition; they also absorb fatty globules, more or less considerable in size, exactly as the epithelial cells and the leucocytes of the larynx and the trachea are filled, simply by penetration, with granules of lamp-black or other dust. The globules of the colostrum are formed in a similar manner, but very rapidly.

* A, Glandular lobule of the mammary gland, with the milk flowing from it. B, Milk-globules. C, Colostrum. *a*, Cells with very distinct fatty granules. *b*, The same, whose nucleus has disappeared. 280 diam. (Virchow.)

In cow's milk, on the contrary, the fats and caseine are predominant: while mare's and ass's milk resemble human milk more closely.

The secretion of milk is essentially intermittent, and takes place only under the influence of special conditions, connected with the function of the genital organs: this function begins in woman at the period of parturition, producing first the colostrum, and, afterwards, the genuine milk. During its long periods of repose, the gland becomes atrophied, as it were; this is its normal condition in young girls, in aged women, and in men. It develops in women at the period of puberty, but the mammary *culs-de-sac* and their globular epithelium become distinct and well-defined only under the influence of pregnancy and parturition; the moulting, which produces the milk, is only the last stage of this hypertrophy. Direct excitation, under some peculiar circumstances, may, however, give rise to this hypertrophy and moulting: young unmarried women, on giving their breast to a nursing child, have found this gland develop and produce milk, under the exciting influence of suction, and a similar phenomenon has been known to occur in the case of men. Finally, at birth, both male and female children, by means of this same rudimentary gland, secrete a fluid strongly resembling milk, and which, no doubt, has some connection with the existence of a similar fatty secretion (*vernix caseosa*) spread over the whole surface of the body.

These different phenomena, the first especially, prove that the mammary secretion is a reflex phenomenon, but experimental physiology has not yet pointed out through what nervous organs this action takes place: experiments on the intercostal nerves, and on the branches of the sympathetic nerve, have yielded no results.[1] As might be supposed, the food appears to have great influence on the production and the character of the milk. Finally, it has been observed that many medicines administered to the nurse reappear in the milk, and this circumstance affords an excellent though indirect method of acting upon the child.

Messrs. Mayensen and Bergeret have, therefore, by a very simple method of analysis, decided that a single, very small dose, of mercury or mercurial salts will be eliminated in a great measure in the lacteal secretion; the *mercurialization*

[1] See Cl. Bernard, "Liquides de l'Organisme." Vol. II. p. 220.

of the nurse of a syphilitic child is, therefore, a very convenient treatment.[1]

Milk forms the type of a *perfect aliment* (see p. 209), being, for a considerable time, the only food of the child; the case is the same with regard to the *egg*, which forms a similar aliment for the bird. All the elements necessary to nutrition have been found, by analysis, to exist in milk (see above) as well as in the egg: salts, hydrocarbons, and albuminoids. The proportions of these various substances in milk are not, however, exactly the same as have been generally supposed necessary to a properly *mixed* diet. It is generally admitted (Moleschott, Voit) that an adult consumes 320 grms. of carbon and 21 grms. of nitrogen, or, in other words, 130 grms. of albuminoid elements, and 488 grms. of hydrocarbons and fats (fats 84, hydrocarbons 404); it follows that, in this case, the normal proportion, in a mixed diet, of nitrogenous to non-nitrogenous aliments, is 1 to 3.7, while in milk, as well as in the egg, the proportion is 1 to 3, or, even, 1 to 2: in other words, the quantity of albuminates (nitrogen) is much larger, and of hydrocarbons (carbon) much smaller. This fact may be easily explained, by referring to what we have already said (p. 78), as to the importance of the hydrocarbons, in regard to the production of force, muscular force especially: the adult draws his forces from the combustion of non-nitrogenous substances, the albuminates scarcely serving for this purpose. On the other hand, when the organism is in course of development, the nitrogenous substances are indispensable to the growth of the different tissues. It is, therefore, easy to see how mistaken is the common practice of condemning children to a diet containing a large quantity of starch, and scarcely any nitrogen.[2] The differences in composition of the milk of the different mammals (see above), are probably connected with the greater or smaller quantity of living force which the young animals possess at birth: thus young calves and colts walk and run almost immediately; therefore, they must, at the very first, produce a considerable amount of force, and we have seen that the milk of the cow and the mare contain a large proportion of hydrocarbons (fat in the cow, and sugar in the mare and the ass). Similar differences are also observed in the eggs of different birds.

[1] See "Journal de l'Anat.," de Ch. Robin. Janvier, 1873.
[2] Wundt, "Physiologie." Trad. de A. Bouchard.

III. *Nervous functions of the skin.*

The skin also possesses extremely varied functions, owing to the numerous nerves terminating in it. We have already studied the centrifugal nerves which innervate its smooth muscles, and cause their contraction under reflex influence (erection of the nipple, for instance), or which terminate in the glands, and give rise to their secretion, this influence appearing especially in the case of the sudoriferous glands.

The skin, however, possesses the greatest number of centripetal or sensory nerves. These have, sometimes, general functions which it is difficult to specify, such, for instance, as their influence as centripetal organs and starting-points to the respiratory reflex action (see *Respiration*, p. 337). The skin is, however, the chief seat of sensation. The epidermis of all those parts of the skin which are extremely sensitive, exhibit special features (papillæ) connected with this sensitiveness. Diseases of the epithelium have, therefore, a great effect on the nervous system: we have already studied the derangement produced by the chill which follows a too great evaporation of sweat; these derangements are, perhaps, often only a nervous reaction, or reflex phenomenon, chiefly affecting the vaso-motors of different organs; pathology is more and more tending to admit this, in order to explain what was formerly dignified with the name of *metastases* (see p. 51).

The study of the sensory functions properly so called of the skin, viz. *feeling* and *touch*, will serve better as an introduction to that of the organs of the senses, properly so called.

PART NINTH.

ORGANS OF THE SENSES.

Our internal as well as our external surfaces are subject to the influence of exterior agents: most of these, under the form of mechanical, physical, or chemical excitants, affect the peripheral origins of the centripetal or sensory nervous system, and give rise to nervous phenomena, the greater number of which we have already studied with that system. Thus we know that there are impressions which may pass unperceived by the cerebral centre, of which we are *unconscious*, and yet cause reactions by their reflections in the medullary system. These impressions and their results belong to the system described by Marshall Hall under the name of *excito-motor* system, and by Magendie under that of *unconscious* sensation or sensibility, and which we have studied under the name of *reflex* phenomena: such, for instance, is the sensation which causes the saliva to be secreted; and such also are the phenomena which give rise to the pulsations of the heart, for we have seen that this organ contracts under the exciting, or rather excito-reflex, influence of the blood upon its walls.

In studying the nervous system, we have also pointed out what is understood by sensation, or *sensibility* properly so called (p. 55). We have seen that the phenomena of sensation may be divided into phenomena of *general sensibility*, comprising the sensations which warn us, in a vague (sentiment) or more or less well-defined (sensation) manner, of the changes taking place in our bodies; and of phenomena of *special sensibility*, which, occurring in special organs, inform us by the modifications produced in these of certain special qualities of the objects by which we are surrounded.

It must not, however, be supposed that the boundary between these two classes of sensations is strictly defined; on the contrary, a certain confusion exists between them, produced by the infinite number of transitionary sensations; thus, for instance, one impression will be perceived for two or three reflex phenomena which will pass unperceived; and thus the stomach, which generally has little sensibility, sometimes in a physiological state becomes extremely sensitive to the presence of food or of foreign bodies.

Now that we know both the character of the phenomena of sensation, and the surfaces which form their starting-point, we will take up the study of general and special sensations experienced at each of these surfaces.

I. GENERAL SENSATIONS.

The general sensations are very widely diffused. Many surfaces give rise to those kinds of sensation only, which give no indication as to the character or qualities of the bodies which make the impression; but show their influence only by impressions which it is difficult to define, such as *pleasure* or *pain*, or even by effects which are still less easily described, and which belong in a great measure to the class of reflex phenomena, such as *tickling*, for instance.

The *mucous surfaces* in general yield only extremely vague sensations. The digestive mucous tissue gives little indication as to the form, the temperature, and other properties of the bodies brought in contact with it, excepting only its upper portion (the mouth) where it exhibits a special arrangement, by means of which it becomes the seat of a special sensation, and constitutes the organ of a sense (taste) which we shall presently study. In cases of fistula of the stomach or intestines, however, various substances have been introduced into these tubes, and their internal surface touched with different excitants, without the patient experiencing any distinct perception, or any sensation resembling those which we shall examine under the name of *touch*.

The vague sensation which warns us of the need of food appears to be a gastric sensation: the seat of *hunger* is supposed to be in the upper part of the digestive tube; we have already seen, however, that this sensation is connected with a general feeling of discomfort, and that it is a call from the impoverished blood for nourishment. The ground of this

opinion as to the seat of hunger is, perhaps, only in our knowledge of the fact that this sensation ceases when food is introduced into the stomach.[1] The case is the same in regard to *thirst:* the sensation of dryness of the throat is caused by a diminution of secretion in these parts, as well as throughout the organism, in most cases this dryness being accompanied by a diminution of the sweat and urine. The sensations accompanying *satiety* are also purely general, being sometimes agreeable and sometimes disagreeable, and having, properly speaking, no fixed seat: indeed, hunger and thirst are sometimes experienced in the highest degree, especially in pathological cases, and in cases of non-absorption, in spite of the ingestion of large quantities of food and drink.

The sensations belonging to the other extremity of the digestive tract are more distinct: that, for instance, known as the desire for defecation, the seat of which is not, however, easily defined. It is generally supposed to be situated in the rectum, but it seems more likely to belong to the intestinal tube, as shown by cases of abnormal anus (see p. 278). This sensation indicates simply that the rectum is ready to evacuate the substances with which it is filled. The defecation which follows is an entirely reflex phenomenon, which we have already studied at length. The agreeable sensation which follows defecation is caused by the overcoming of a difficulty; in place of this, however, in cases of irritation of the intestine or rectum, a peculiar and painful sensation is sometimes experienced, known under the name of *tenesmus*, producing a desire to throw off the fecal matters even when the intestine is completely empty.

A foreign body produces scarcely any distinct sensation *in the mucous of the pulmonary organs:* its hardness, its form, and its temperature, are felt very slightly if at all; it, however, produces a vague sensation of pain and uneasiness, and immediately causes a reflex action, giving rise to an involuntary cough, for the purpose of expelling the offending

[1] "I have questioned a number of soldiers on this point, choosing carefully those who were ignorant of anatomy, in order that their replies might not be influenced by any involuntary localizing of the sensation. Several among them vaguely indicated the neck or the chest as the seat of hunger, twenty-three indicated the sternum, four could not trace the sensation to any particular spot, while two only designated the stomach. These latter were hospital nurses, and had, consequently, a few ideas in regard to anatomy." Schiff, "Physiologie de la Digestion."

substance. The presence of bodies in these organs is often only discovered after death. The pulmonary surface, properly so-called, appears to be the seat of agreeable sensations (breathing pure air) as well as disagreeable ones (breathing vitiated and confined air); these are, however, in reality, more widely diffused, and, moreover, like hunger and thirst, are connected with the need of the entire organism for a greater or less quantity of oxygen.

The lung may even be said to be much less sensitive than the intestine; we have seen that the latter, in pathological cases, becomes extraordinarily susceptible to impressions; the lung, on the contrary, in a similar case, gives no sign of being diseased, unless the neighboring parts are affected, the pleura, for instance (*pleuritis*); in general, however, the maladies of the pulmonary surface occasion little pain, and only give rise to a sensation of dyspnœa, a vague feeling of discomfort, the seat of which is so little understood that people commonly attribute it to the stomach.

The *genito-urinary mucous*, that we shall study later, most usually presents only a dull sensation, always subjective, ordinarily unlocalized, and in no wise informing us what cause excites it. Properly speaking, there is no sensation or sensibility in the kidney, testicles, or ovary. We will analyze, farther on, the desire to urinate; we shall find it wholly similar to that for defecation, and shall see also that it is in no less a degree specially localized, and is composed of extrinsic sensations, that we never perceive in those parts where they are actually produced. The sexual desire may, on the one hand, be compared with the desire to urinate, and, on the other, with the desire to breathe, with that of hunger or of thirst, for instance; it is a general desire, produced under the influence of a great number of circumstances, as much internal as external, and that we localize in the sexual organs, because we know the phenomena which take place in them, and that are apt to calm the desire.

The emission of spermatic fluid is accompanied with an agreeable sensation that we refer to the terminal portion of the canal of the urethra, but whose seat is but ill-defined, being situated, like that of the desire to urinate, in the deeper portion (prostatic region), because individuals whose glans has been amputated refer their venereal sensations to the navicular fossa of the urethra which they no longer possess.

The womb has equally a mucous surface of dull, and almost entirely reflex, sensibility, the most important of

whose uses is the expulsion of the fœtus; this is also accompanied with violent pains, characterized always to a greater or less degree by energetic contractions of the smooth muscular fibres. The expulsion is followed by a sentiment of a difficulty overcome, as is that of micturition and defecation, etc. The neck of the womb does not even partake, in spite of numerous nerves, of the sensibility to pain; it can only be the point of departure for certain reflex phenomena: thus it can be cauterized or incised without provoking any sensations; cancer of this organ can become painful only by the development of what we have designated as sympathetic or reflex sensations, and, better still, as associated sensations (p. 57) which radiate towards the sacrum, the thighs, the abdominal walls, etc. (lumbar and sacral plexus).

In order to complete the study of general sensations, we must here say a few words as to the sensibility of the various tissues connected with the surfaces, or placed between them in the deeper portion of the organism. As might be supposed, the *muscular*, *connective*, *bony*, and *glandular tissues*, *have either very little sensibility*, *or none at all.* The muscle may be cut or burned, without producing any very painful sensation, while, if greatly distended, or strongly contracted, it becomes the seat of peculiar vague and painful sensations, such as *cramps*, which are generally experienced chiefly in the smooth muscles (intestinal, uterine, vesical, colic, etc.). In cases of inflammation this tissue becomes extremely sensitive, as do also the bones, the tendons, the articulating ligaments, and the tissue of the glands themselves. This pathological sensibility is, no doubt, caused by the fact that inflammation, which has a tendency to destroy the organs (especially the muscle), also attacks the nerves contained in them; and because the swelling which nearly always accompanies this pathological process, distends the nerves of the tissue itself, and those of the adjacent tissues, and thus occasions their hyperesthesia: this is the reason that the glands are extremely sensitive to compression, and very painful when swollen.

The muscle appears to possess a peculiar sensibility which forms a sort of transition from general to special sensations; this is what is called the sense of contraction, the muscular sense, by which we know *that we have executed movements.* What the mechanism and the organs of this sensation may be, is not yet decided (see, farther on, *Pacinian corpuscles*

of the muscles), but the *muscular sense* is none the less an indisputable fact.[1] Cl. Bernard has made it certain by various experiments: if all the cutaneous nerves of the limb of an animal be cut, the skin is rendered completely insensitive, although the animal still continues to walk tolerably well, probably because the muscular sensibility is preserved. If the posterior roots (that is, all the sensory nerves, muscular and others) are cut, instead of the cutaneous branches, the movements made by the animal become much less steady. In cases of extensive paralysis in man, when the sensory branches of the muscles are implicated, the patient appears to move his limbs with difficulty, and to be able to do so, only when watching them so as to direct their movements (Cl. Bernard). Finally, some pathological observations have been made in which paralysis of the muscular sense was observed, while the sensibility of the skin remained, or *vice versâ* (Landry, Axenfeld). This sensibility, or rather *muscular sense*, enables us to judge of the *force* and *extent* of our movements: we judge of their force by distinguishing the difference between different weights, raised one after the other, provided that the variation in the weight of each be at least $\frac{1}{17}$ (Weber); and it is remarkable that the sensibility for lifting weights is much more acute than for the pressure produced by such weight (see farther on, *sense of touch*); this proves once more that the sensibility of the muscles is entirely distinct from that of the skin.

The study of the muscular sense is still, however, wrapped in such obscurity that some authors (Trousseau) have entirely denied its existence, while others differ greatly in their opinions respecting it: thus Wundt maintains that "the seat of the sensations of motion appears to lie, not in the muscles themselves, but rather in the motor-nerve cells (of the anterior gray matter of the spinal axis), since we experience not only the sensation of a movement performed, but also that of one which has been only intended: the sensation of movement thus appears to be directly connected with motor innervation" (for which reason Wundt designates it as the *sensation*

[1] See Duchenne (de Boulogne), "De l'Electrisation Localisée," p. 389. Paris, 1872.

Cl. Bernard, "Leçons sur la Physiologie et la Pathologie du Syst. Nerveux." Vol. I. p. 246.

Jaccoud, "Les Paraplégies et l'Ataxie du Mouvement." Paris, 1864.

of innervation).[1] It is, however, probable that this sensation, by means of which we are made aware of the degree of contraction of our muscles (*sense of muscular activity*, Gerdy) is the same as that which causes the sensation of fatigue which follows moderate but long-continued exercise, and that its seat lies in the contracted fibres, while the sensation of fatigue experienced after violent exertion appears to reside principally in the tendons (Sappey).

II. SPECIAL SENSATIONS.

The *special sensations* render us conscious of external bodies, and of their various properties. They are furnished by the organs *of the senses*, each of which supposes, 1, an *organ susceptible* to the impression; 2, a *nerve*, by means of which the impression is transmitted; and 3, a *central part* of the brain by which the impression is received and understood.

The peripheral organ, which first receives the impression, proceeds always from a more or less modified part of the cutaneous and external surface (epidermis), or of the most primitive parts of the internal surface (epithelium): thus we have, as organs of the senses proceeding from the skin, the

[1] See also researches by Bernhardt (Zur Lehre von Muskelsinn. Analysé, en "Revue des Sciences Médicales," de G. Hayem. Vol. I. p. 61, 1873). This author holds, with J. Müller, Ludwig, and Bernstein, that the muscular sense simply consists in the faculty of exactly estimating the intensity of the excitation which, beginning in the encephalon, results in the movement intended. He found, after causing the contraction of the muscles by faradization (the interrupted current) that the person experimented upon experienced much greater difficulty in recognizing the variation between different weights than when the contraction was produced by the influence of the will. From this Bernhardt concluded that the sense of force is a *psychical function*. He admits, however, that the sensory impressions beginning in the soft parts adjacent to the muscles have a powerful influence in completing the notion or idea formed by the centres of volition. According to him, therefore, the muscular sense, properly so called, has no existence. Trousseau, considering the subject from a similar point of view, has also denied the existence of the muscular sense, referring every thing to the sensibility of the soft parts displaced by the movement. See Art. *Ataxie*, en "Nouv. Dict. de Méd. et de Chir. Prat." Vol. III. p. 776.)

organs of *touch*, *sight*, and *hearing;* and, from the initial parts of the digestive and the respiratory mucous surface, we have the organs of *taste* and *smell.*

I. Feeling and Touch.

This is a *mixed sense*, for it enables us to recognize, 1, the *pressure* exercised by different bodies upon the integuments, and, 2, the *temperature* of these bodies.

The organ of touch includes the whole external integument and a part of the mucous surface, especially of the *primæ viæ*, the mucous surface of the alimentary canal (the tongue and also the teeth). These organs are formed of two parts essential to every integument, the *epidermis* or *epithelium*, and the *dermis;* the epithelial covering, indeed, is indispensable to touch, and if its globular elements are injured or destroyed, the sense of touch ceases simultaneously. By means of its growth towards the exterior, the epidermis forms crests, or hollow papillæ, into which the dermis penetrates, bringing with it the vessels and the nerves; we are still, however, unable to explain exactly this indispensability of the epidermis, since the nerves appear to terminate in the dermis, and their connection with the epithelial globules are still hypothetical; although it has been demonstrated in the case of certain organs (as we shall see in regard to the nasal chambers and the internal ear); it is, however, certain that the more delicately formed, and highly developed is the covering of the papillæ, the more exquisite is the sensibility of the papillæ. Some important growths of the epidermis even appear to be essentially connected with the exercise of the sensation of touch: the teeth, which are extremely hard, and covered with a thick layer of modified epithelium (the enamel), are nevertheless the seat of the most delicate sense of feeling; cats feel with the long hairs growing from their mouth (see p. 431: tactile hair); insects have horny feelers; the sole of the foot is covered with a thick layer of corneous epidermis, and yet its sensibility is exquisite. The thickness of the epidermis is, therefore, no obstacle to the sensibility of the skin.

The papillæ of the dermis contain the terminations of the nerves; the papillæ do not, however, all contain nervous elements, many of them having only vascular network (Fig. 101, B, C, D); the papillæ of the dermis are more highly developed in proportion to the exquisite sensibility of the

part; in the tongue, for instance, they have a finger-like formation, or exhibit numerous divisions. It was formerly supposed that the nerves in them terminate in loops; but now that small terminal organs, especially adapted for the purpose, have been discovered, this latter view is being gradually adopted; and indeed these tactile organs are being constantly met with in parts where their presence was not in the least suspected. These terminal organs are small ovoid bodies, or *tactile corpuscles* (of Meissner and Wagner), generally of the shape of a *pineapple*, or of some simpler and less regularly formed shape (*corpuscles of Krause*), at the base of which we find from 1 to 4 nerve filaments which penetrate, and appear to be lost in the substance of the corpuscle (Fig. 101, A). If these nerve threads are cut, the

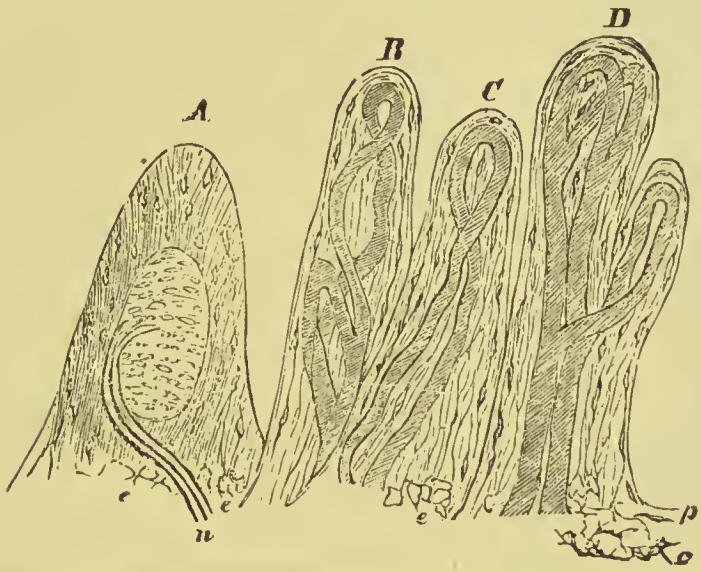


Fig. 101. — Vascular and nervous papillæ of the pulp of the fingers.*

sensibility of the papillæ containing the corresponding terminal organs ceases, and these organs change into a small mass of fat; in persons whose sensibility is paralyzed, only small drops of fat are found in the place of these organs;

* The epidermis and Malpighi's network have been removed. A, Nervous papilla, with a tactile corpuscle, into which enter two primitive nerve fibres, *n*; at the base of the papilla are seen fine elastic nets, *e*, from which proceed fine fibres; between and in the midst of the latter are seen corpuscles of the connective tissue. B, C, D, Vascular papillæ, simple at C, with loops formed by anastomoses of vessels in B and D. Near these vessels are seen fine elastic fibres and corpuscles of the connective tissue. *p*, Papillary body, having a horizontal direction. *e*, Stellate elements of the corium. 300 diam. (Virchow.)

from these facts the tactile bodies, etc., would seem to be the seat of sensibility.

We also find larger corpuscles in the sub-cutaneous connective tissue and deep in the dermis, hanging from the nerve tubes like fruit from the twigs of a tree, and visible to the naked eye. These are the *corpuscles of Pacini:* they are surrounded by several fibrous envelopes (Fig. 102), and have an elongated cavity in which one or several nerve filaments terminate in a manner not yet perfectly understood. They are found chiefly in the palm of the hand, in the path of the collateral nerves of the fingers; their presence in various other organs, however, especially in the mesentery of the cat, leads us to doubt their value as organs of tactile sensibility.



Fig. 102. — Pacini's or Vater's corpuscle, taken from the adipose tissue of the pulp of the fingers *

Kölliker has attempted to prove that these various corpuscles all belong to the same type, being composed of similar essential parts, namely, 1, terminal nerve fibres (one or several pale tubes), one end of which is always free, and often enlarged in the shape of a club; 2, an internal bulb or central mass, formed of a kind of connective tissue, and serving as a support or envelope of the nerve fibre; 3, an enveloping sheath of connective tissue.

Rouget is very justly opposed to this idea of the assimilation of the various corpuscles; his histological researches have convinced him, 1, that there is no real analogy between the structure of the *tactile corpuscles* (and the *corpuscles of Krause*), with

* Primitive nerve fibre, containing medullary substance, *n*, having a marked outline, and a thick nerve sheath, *p*, *p*, which contains longitudinal nuclei, and forms the tail of the corpuscle. C, The corpuscle proper, with its concentric layers formed by the envelope of the nerve swollen into the shape of a club, and having a central cavity, into which the axis-cylinder passes and is terminated. 150 diam. (Virchow.)

the Pacinian corpuseles; 2, that the tactile eorpuscles and those of Krause are only secondary forms of the same type; and, finally, that this type, in opposition to that of the Pacinian corpuseles, presents the closest analogy to the fundamental structure of the termination of the motor nerves.

The form of the eorpuscles of Krause, as observed in the eonjunctiva, appears to be that of the most elementary of the nerve terminations: it eonsists of a nerve tube, with a double outline, rolled up at its terminal portion, and deprived of its medullary layer, swelling out as it loses itself in a mass of nerve substance, exactly similar to that of the axis-cylinder, containing central nerve cells; this tube is furnished with nuclei, and has as a covering only the prolongation of the sheath of Schwann. The same type is found in Meissner's or the tactile eorpuscles: round the central portion the nerve fibres are rolled up, with no interstiees between them, and transversely strewn with elongated nuelei, and thus the corpuscle gets that peculiar appearance which has been likened to that of a pineapple, but which, according to Rouget, resembles much more an ovoid and cylindrical ball of twine: "errors in observation have led to the belief that the nerve tubes terminate either in loose ends, or loops, on the surface of the corpuscles. Beginning at the base of the papillæ, the nerve tubes emanating from the sub-cutaneous network turn towards the axis and join the tactile corpusele, either at its lower extremity or at its middle portion; sometimes passing along the borders or the surface, they extend nearly to its lower portion: if the plaee at which the tube with the double outline appears to cease be carefully observed, we find that, losing here its medullary layer, and the peculiar refraction belonging to it, the gray, pale nerve fibre glides into the interstiee between the transverse striæ of the corpuscle, and disappears more or less suddenly from sight, penetrating the interior of the cortical layers. In the central mass of the corpuscle, the gray fibres with nuelei are not found, nor the tubes with a medullary layer: this central mass is composed of a finely granulated and extremely refracting substanee, furnished with nuclei, and exactly similar to that which forms the nerve off-shoots of the conjunctiva. . . . It is extremely probable that, as in the ease of the ganglionie eorpuscles, the terminal plates, the terminal end of the electric plates, etc., this is only a swelling or opening out of the peculiar nerve element, the *axis-cylinder*."

The short, gray, horizontal, and ribbon-like fibres, twisted

round a central mass of nerves, form the elements which take the place of the three portions of which the tactile corpuscles of feeling were formerly supposed to consist. The transverse nuclei belong to the sheath of Schwann.

On the other hand, the corpuscles of Pacini and Vater are found in parts of the organism in which they can be of little use in respect to touch, properly so called: we find them, not only in the mesentery (see above), but also in the nerves which go to the bones, and even in the interior of the muscles. They appear to be extremely sensitive to compression, and their function is, no doubt, connected with this mode of sensibility: for instance, their sensations indicate the degree of contraction of the muscles, according to the compression which these muscles produce upon them. They are also subjected to other kinds of pressure: thus the corpuscles situated in the articulating capsules are compressed by the bones in certain movements, and also by the tension of the ligaments; in the mesentery, they are compressed by the abdominal muscles, acting upon the walls of the viscera; their superficial position, under the integuments, is favorable to the transmission of external pressure (Rauber).[1]

The functions of touch are most highly developed in those parts which contain the largest number of nerves and tactile corpuscles: thus the organs which we chiefly use are the hands, the tongue, and the teeth, not forgetting the sole of the feet, which is a constant organ of touch during walking, and which, judging of the character of the ground, causes and modifies the reflex action of locomotion, almost without any exercise of the consciousness or of the will (see p. 48). The parts in which the sensation of *pressure* and of *temperature* reside are not exactly the same, although it is impossible to point out the cause of this difference.

The *sensation of temperature* is almost generally diffused over the whole surface of the body, and it would seem at first thought as if no part is more privileged in this respect than

[1] The sensation and the measure of contraction of those muscles in which these corpuscles are not found is produced by other special methods of arrangement. This is the case in regard to the muscles of the jaw, and the teeth, the muscles of the eyelids, the conjunctiva, etc. A fact which seems to show the independence of the muscular sensations on the sensibility of the skin is, that if this sensibility is diminished by means of cold, the sensations of muscular contraction continue or are even increased. (Rauber, Dissert., Munich, 1865. See above, pp. 389 and 390.)

another; it is, however, commonly observed that the heat of the body is best judged of by the lips, the cheeks, and the back of the hand: a physician, who desires to ascertain the temperature of a patient's skin, tries it with the back, not the palm of the hand; for the same reason, if we wish to discover if some imperceptible drops of rain are falling, we put out the back, not the palm of the hand. This sense of temperature acts only through comparison; it does not indicate the temperature of the skin, but only the rise or fall of the temperature; for instance, we are conscious of the difference in temperature between our hand and forehead only at the moment when we touch the forehead with the hand.

In order to bring this thermal sensibility into play, the temperature to be ascertained must be between 0° and 70° (C.); outside of these extremes only painful sensations of cold or heat are felt, and we are unable to judge of the difference of a few degrees: we judge best of a slight variation in the temperature of a body when between 30° and 50° (C.); in other words, the temperature is more easily ascertained the nearer it approaches that of our own body, and also if a considerable part of its surface be compared at the same time; thus a finger dipped into a fluid at 37° (C.), gives an idea of less heat than an entire hand in one at only 30° (C.). Anæmia appears to increase the sensibility of the skin to differences of temperature, while hyperæmia diminishes it.

The *sensation of pressure*, produced in us by different bodies, is very unequally distributed in different parts: it is most acute at the tip of the tongue and the ends of the fingers: thus the *digital extremities* are points in which our sense of touch chiefly lies. In order to decide exactly the degree of sensitiveness of different parts of the body, a pair of dividers is employed (Weber's compass),[1] and the degree of sensibility of the surface is measured by the distance that one leg of the dividers is from the other, when a person can perceive the impression of the two points of contact; the less the distance between them, the greater the amount of sensibility. At the tip of the tongue 1 m.m. of distance is sufficient; 2 m.m. on the palm; and 12 m.m. on the back of the hand: while on the skin of the trunk, especially in the dorsal region, the distance must be 5 or 6 centimetres.

While applying the name of *circle* of sensation to that ex-

[1] See Weber, Art. "Tastsinn" in "Wagner's Handwörterbuch der Physiologie."

tent of the surface of the skin in which the impression made by the two points of the dividers (æsthesiometer) forms only one, we find that the extent of these circles differs greatly according to the parts of the body under consideration; the limit is very small at the tip of the tongue, but increases greatly in the dorsal regions of the trunk; anatomical data also show that this extent is in inverse ratio to the quantity of tactile corpuscles contained in the skin. We must not, however, decide absolutely from this that a circle of sensation has an anatomical breadth or size, such, for instance, as the space enclosed by the ramifications of a nerve fibre: in order to prove the contrary, it is sufficient to remember that the extent of a circle of sensation varies according to attention, exercise, habit, and other influences. Since the space which is between the points of the dividers, in certain parts, contains more than twelve of Krause's corpuscles, while in these parts two circles of sensations meet, or even partly overlap each other, so that they cannot be separated by *perception*; we must admit that these are phenomena of *radiation*, that is to say, that the excitation of sensory nerve fibre is transmitted to other adjacent fibres; and since attention, habit, and exercise can diminish this radiation, we must conclude that it is not an instance of *peripheral impression*, but of *central perception*.

In regard to the skin of the various segments of the limbs, especially of the arm, Vierordt has arrived, by means of numerous and careful experiments, at the conclusion that the sensibility (*sense of touch* or *sense of localization*) varies in proportion to the distance between the point considered and the articulation immediately above it, going back as far as to the root of the limb. The comparative values of the delicacy of the sense of localization also form the sum of two breadths: the one, which is constant, being the sensibility of the skin in the axis of the articulation; the other, which is variable, being in proportion to the distance between the point under consideration and the articulation situated below it, and, therefore, in proportion to the extent of the movements of localization around the articulation.

One remarkable circumstance, which may be easily explained by referring to our study of the nervous system is, that prolonged sensations of pressure last for a considerable time after the causes producing them have ceased to act: persons who wear spectacles feel them still after taking them off; and after holding an object in the hand, we sometimes

seem to feel it long after we have let it go. This is a kind of echo of sensation, and is purely subjective.

The manner and form in which the sensation of pressure is produced by different bodies give us such exact information as to their nature, that we might, without close examination, suppose this to be the result of special sensations. Thus, we judge if the surface of a body is smooth or rough, if it exhibits any anfractuosity (peculiar conformations), by the way in which it presses upon our digital extremities; by passing our fingers over surfaces we judge of their form. The variations of pressure, and the reactions of a body in opposition to efforts which we ourselves make, enable us to judge whether it is hard or soft: we judge in the same way whether it is in large pieces or dust; whether it is solid or liquid: in short, we obtain precise ideas as to the condition, the form, and extent of the body.

Differences of pressure also enable us to judge of the weight of a body; but it must be admitted that the muscular force necessary to counterbalance the weight (see p. 453) is of chief importance in our estimate.

Finally, the sensations of pressure, form, weight, and temperature, are often connected with each other; thus, of two equal weights, the colder will seem the heavier; if we place upon our forehead two five-franc pieces of different temperature, the warmer will appear to be the lighter. On the other hand, smooth bodies appear to be colder than those of uneven surface, and, subjectively, they really are so, because, their surfaces being unbroken, more caloric is drawn from us.

The most striking example of the perfection to which the sense of touch may be brought, is found in the case of blind persons, who learn to distinguish colors by touch; as they do this solely by means of the different degrees of roughness, they are unable to distinguish natural colors whose surface is equally smooth.

Finally, the sensations, whether general or special, produced by the skin, are reduced to three: contact (or pressure), temperature, and pain. The nature of these three kinds of sensations, and the manner in which they are produced, are as yet undecided; as loss of sensation to one may exist, while sensation to the others remains intact, we are led to suppose that a separate class of nerve fibres belongs to each, and that pain, for instance, has not the same path of conduction as sensations of touch, while the latter follow other conductors than those of the sensations of temperature.

We have already seen that Brown-Séquard (p. 46), allows that these isolated conductors are found in the spinal axis, and that he estimates their number as four, belonging to temperature, pain, touch, and tickling (mention is made of the *muscular sense*, which is entirely distinct from these, its conductors being found in other strands of the axis).

The difference in sensations may, however, be simply owing to the specific energy of the terminal nerve organs, some of which (corpuscles of Pacini) govern the sensations of pressure, and others (tactile corpuscles), those of touch, or what is called the sensation for localization in the skin; while others (still more difficult to define) regulate the sensations of temperature and pain. If this be the case, a special excitant will produce the corresponding special sensation only when applied to these nerve terminations, and not when it reaches the trunk of the nerve, the fibres of which form similar conductors. Thus if the elbow is dipped into cold water, the ulnar nerve, excited by this change of temperature, will occasion sensations extending to the inner side of the hand (see p. 56); the sensation experienced in this case, in the little finger, consists of a vague and undefined feeling of pain, not of cold, which would be the case if the hand were dipped in cold water.

According to some authors, these sensations are only higher or lower degrees of an excitation the nature of which is always the same; looked at in this light, pain is only the highest degree of excitation of the skin, whether by pressure or by change of temperature; while any excitation, of whatever nature, will excite the same sensation in a lower degree; thus, if a part of the skin be covered with a card, in which a very small hole is made, and an excitant of any kind brought to bear upon that portion of the skin which is exposed through this hole, there will be no difference between the sensations produced, whether they be caused by the application of a red-hot coal, the prick of a pin, or by tickling with a feather, etc. In spite of this experiment, however (experiment by Fick),[1] we can hardly admit that all these sensations are of the same kind, and differ only in degree, when we see that in certain pathological cases they may be independently paralyzed, or that special subjective sensations may be produced. It is especially difficult to admit that pain is only

[1] See H. Taine, "De l'Intelligence." Paris, 1870, Vol. II. Book III. *Sensations du Toucher.*

the result of excitation carried to the highest degree, for many instances are known of the sensibility to pain ceasing entirely (analgesia), while all other forms of sensibility (touch, tickling, to temperature) remained: in this case we must conclude that the nerve terminations have lost their susceptibility to the higher degrees of excitation, while they are still capable of being affected by the lower.

II. The Sense of Taste.

The *sense of taste* is the result of special impressions produced by certain sapid substances; it is, however, difficult exactly to define a sapid substance, and to analyze the interior phenomenon of the impression produced by it; there is, also, some difference of opinion in regard to the subject of distinguishing between the true sapid substances, and those which only excite the general or tactile sensibility of the organ of taste.

The exclusive seat of *taste* is in the *mouth*. The *palate* is commonly spoken of as the seat of this function, but physiological experiments have proved that the sense of taste, *par excellence*, resides only in the *tongue*, and is even restricted to certain parts of this organ. In general, when we wish to taste any substance, we place it upon the tongue and apply the latter to the palate, in order to compress the sapid substance, and thus increase its points of contact with the gustatory surface; it is on account of this that the palate has been wrongly supposed to have an office to perform in tasting in addition to this simple mechanical duty.

A fruitful cause of mistake, and one which ought to make us distrust many experiments, lies in the fact that sensations have been often mistaken for *taste*, while these were only produced by the *general* or *tactile sensibility* of the tongue. We have seen that this organ, especially its tip, must be classed as the most important among the organs of touch: certain sensations, dignified with the name of tastes, are caused by this sensibility, such as the farinaceous savor resulting from the mechanical impression produced by a substance divided in small pieces, and the *gummy taste* of substances in a more or less sticky condition. What is known as a *fresh* or *cooling taste*, is only the thermal effect produced by the absorption of caloric, caused by a substance in dissolving (such as the taste of nitre), or in evaporating (as the taste of the essential oils). We speak also of *acrid*

tastes; but these are a feature of general sensibility: a substance of an acrid taste has a tendency to destroy the mucous surface, as if by a blister; we therefore designate as acrid those substances which modify, eat into, or dissolve the epithelium.

On the other hand, sensations arising only from some impression made upon the organ of smell are frequently mistaken for gustatory impressions; the organs of taste and smell are situated so near each other, that it would seem that their sensations must be connected. *Aromatic*, *nauseous* sensations, etc., belong to this class: thus roast meats, cheese, some vinous and other drinks, owe their sapid properties to the development of fatty acids or peculiar odoriferous ethers. If we stop up the nostrils while eating, or have simply a cold in the head, we find that most alimentary substances lose their taste.

It is more difficult to decide whether *salt*, *alkaline*, and *acid* savors are actually gustatory sensations, or sensations of touch in a disguised form. Schiff considers them to be really gustatory impressions, because they are not perceived as such when the cutaneous surface is excoriated, and also because they are produced by the exciting influence of the galvanic current: we know that this current gives rise to gustatory sensations which are not caused by the electrolytic decomposition of the buccal liquids, and which consist essentially in an acid taste at the positive pole, and an alkaline taste at the negative pole. However this may be, the acid and alkaline sensations form a transition to the really gustatory sensations.

By excluding all the so-called savors which are produced by such impressions as we have mentioned, we arrive at the conclusion that there are really only two distinct tastes, *sweet* and *bitter*, and only two kinds of really sapid bodies, *sweet* and *bitter*. There is nothing to be said in general as to those substances, between which there appears to be no chemical connection; for we find bodies in the class of chemical substances which, in a chemical point of view, are most dissimilar, such as salts of lead, sugars, properly so called, and a number of alcohols (glycerine).

By experimenting with these substances we find that the posterior part of the upper surface of the tongue, its lower surface, and the frenum have no power to cause sensation of taste; this latter is confined to the edges of the tongue, especially to the tip. In these parts, beside the *filiform* or con-

ical *papillæ* which are everywhere met with, and of which we spoke in relation to the sense of touch, we find two somewhat peculiar forms of papillæ, the *fungiform*, and the *circumvallate* (Fig. 103). The fungiform papillæ somewhat resemble a mushroom, having a short pedicle, and a globular head, in which the dermis forms a number of secondary papillæ, resting in a bed of epithelium, with which the organ is uniformly covered (Fig. 103, B.). The *circumvallate* papillæ resemble these, though they are wider and flatter, and are imbedded in an excavation in the mucous tissue (*calices*), beyond which they scarcely project at all; they also exhibit a number of secondary papillæ, covered by the epithelium (Fig. 103, C.). A number of nerve filaments terminate in these papillæ, but whether by true extremities, by corpuscles similar to those of touch, or by union of the epithelial cells, remains still undecided.[1]

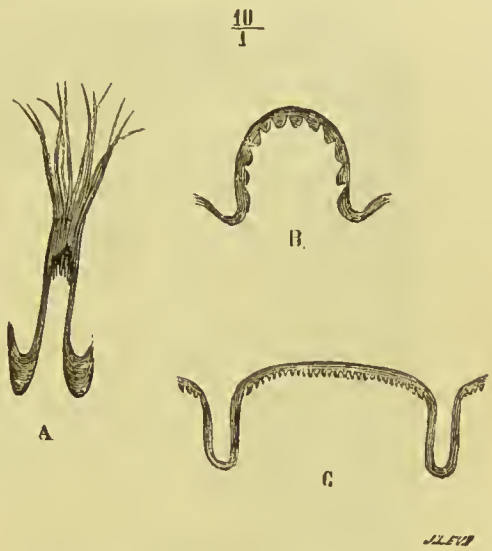


Fig. 103. — Lingual papillæ. (Todd and Bowman.)*

These papillæ are placed upon the back of the tongue, the *fungiform* being arranged in the form of a quincunx along the sides of this organ; their number varies in different persons, the *circumvallate* or *large* papillæ are arranged in two rows, which meet at the base of the tongue (foramen cæcum), in a form like that made by the union of the two arms in the letter V (Fig. 104).

We have already remarked that the sense of taste resides only in those parts in which these papillæ, especially the *circumvallate*, are found, that is, at the base of the tongue; for this reason, tastes are most clearly perceived, and in the most agreeable manner, at the commencement of deglutition, when the alimentary substances come in contact with the V-shaped row. This *row of large papillæ* appears to be the special seat of the impression produced, especially when made by

[1] See Art. Goût, in Vol. XVI. of the "Nouveau Dict. de Méd. et de Chirur. Pratiques." 1872.

* A, Filiform papilla. B, Fungiform papilla. C, Circumvallate papilla.

bitter substances, for when their innervation has been destroyed, the animal will swallow bitter substances without any apparent repugnance. The *sensations of nausea*, which give

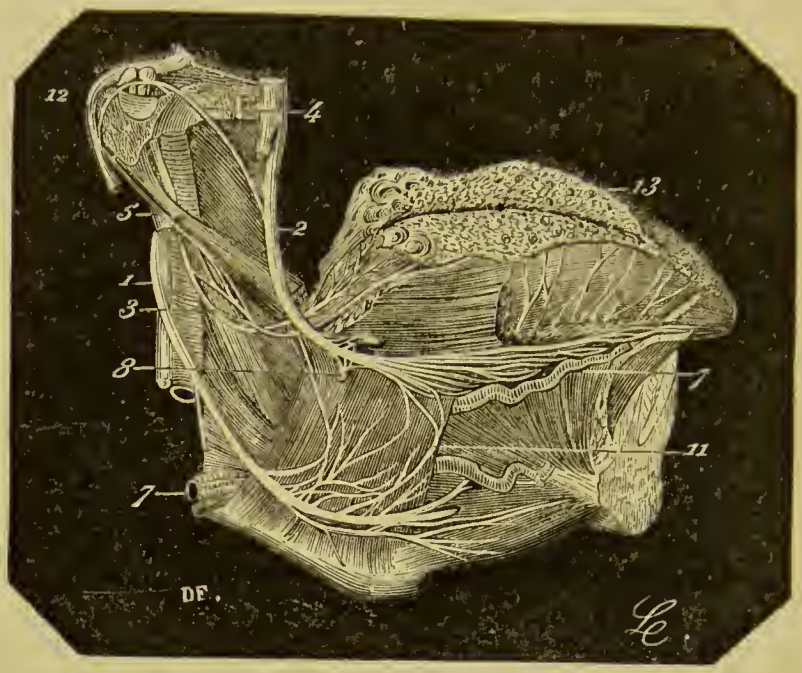


Fig. 104. — Tongue, with its papillæ and nerves. (L. Hirschfeld and Leveillé).*

rise to the antiperistaltic movement of deglutition, of vomiting, also take place chiefly in this part; but these are phenomena of ordinary sensibility, for if the finger be placed at the back of the mouth, this reflex action will be produced, and still better if the uvula be touched instead of the base of the tongue.

Sapid bodies must be dissolved in order to be tasted: the secretion of the saliva is, therefore, necessary to gustation, and if the mouth be dry, the substance received will make little impression. The impressions made by sapid substances are, therefore, peculiarly fitted to produce the reflex phenomenon of the salivary secretion, especially the sub-maxillary secretion, as we know that the sight or remembrance of a favorite dish will sometimes *make the mouth water;* thus, if a piece of meat be shown to a dog, the saliva is seen to flow freely from a tube inserted in the duct of the sub-maxil-

* 1, Hypoglossal nerve. 2, Lingual branch of the tri-geminus. 3, Lingual branch of the glosso-pharyngeal nerve. 4, Chorda tympani. 8, Sub-maxillary ganglion. 11, Anastomoses of the lingual with the hypoglossal nerve. 12, Facial nerve. 13, Mucous membrane detached and thrown upwards: the circumvallate papillæ are seen behind.

lary gland, for which reason Cl. Bernard has suggested that this gland should be considered as essentially connected with the functions of gustation.

The nerves of taste are the *lingual* and the *glosso-pharyngeal* nerves. The lingual, which is a branch of the trigeminus, extends to the posterior part of the tongue, imparting to it general and tactile sensibility, as well as taste. The glosso-pharyngeal nerve extends to the base, and regulates the gustatory sensibility of the large papillæ (Fig. 104). It is this nerve, chiefly, which transmits the impressions made by bitter substances: for this reason it has been called, too exclusively, as it would seem, the *nauseant nerve*. The *lingual* and *glosso-pharyngeal* nerves thus govern equally the sense of taste, and both possess fibres of general sensibility, but that the fibres of feeling or general sensibility are quite distinct from the fibres of taste is apparently proved by the fact that one of these senses (*taste*) may entirely cease, while the *general sensibility* and power of sensation in the tongue continue unimpaired.

The question has arisen whether it would not be possible to separate the fibres of taste from the fibres of toueh in the glosso-pharyngeal and the lingual nerves. No method is as yet known by whieh the former may be separated, but the study of paralysis of the faeial nerve in the posterior part of the tongue, the region innervated by the lingual nerve, this paralysis being aeeompanied by the loss of taste, has led to the belief that the solution may possibly be found by studying the *chorda tympani*, a small nerve thread whieh, beginning in the facial nerve, traverses the middle ear, and joins the lingual nerve at the level of the pterygoid museles (Figs. 105 and 106).

The study of the funetions of the ehorda tympani is one of the most delieate questions. We have already spoken of the offiee of this nerve or eord in referenee to the seeretion of the saliva. We were then seeking to diseover whether all the fibres of this nerve eease at the level of the submaxillary gland, or whether any of them go beyond this, and extend to the tongue. In spite of numerous contradietory experiments, physiologists now nearly all agree in the opinion that the ehorda tympani does extend to the tongue. Vulpian and Prévost have eonstantly found degenerated nerve fibres in the terminal braneches of the lingual nerve, after the chorda tympani had been destroyed, either by being eut in the ear, or by the removal of the faeial nerve: these degenerated fibres can only arise from the ehorda tympani.

The next inquiry to be made was whether the ehorda tympani is united to the tongue as a motor or as a sensory nerve. The latter funetion is now assigned to it by some physiologists, espeeially Lussana and Sehiff, both of whom maintain that the ehorda tympani

is not only a nerve of sensibility, but one of special sensibility, as it is the principal organ of taste. Lussana and Inzani mention ("Archives de Physiologie," 1869 and 1872) the case of a person in whom the chorda tympani had been cut in an operation performed on the middle ear by a quack. After the operation the posterior two-thirds of the corresponding half of the tongue were found to have lost the sense of *taste*, while retaining an unimpaired *sensibility* to *touch* and to *pain*. Lussana has since collected several similar observations in cases in which the paralysis of the facial nerve, following a wound or an operation, was accompanied by the partial loss of the sense of taste. Lussana made the experiment of performing the bilateral extirpation of the glosso-pharyngeal nerves in a dog, and afterwards cutting the two chordæ tympani. The result of this experiment showed that the sense of taste entirely disappeared while the posterior portion of the tongue retained its sensibility to touch and pain. In a counter-experiment Schiff ("Physiologie de la Digestion," Florence, 1866, Vol. I.) succeeded in cutting the lingual nerve above its junction with the chorda tympani, close to the base of the skull; the tactile and painful sensibility of the corresponding portion of the tongue ceased entirely, while traces of the sense of taste remained; these, though sometimes extremely slight, could be always recognized by the movements and contortions of the animal subjected to the influence of acid or bitter substances.

Lussana and Schiff conclude from this, that *the lingual nerve governs only the general sensibility of that portion of the tongue through which it spreads, and has no gustatory fibres of its own, these fibres proceeding from the chorda tympani.*

This conclusion, unfortunately, loses something of its value from the circumstance that it necessitates a condition which it is almost impossible to satisfy in the present state of science. What course do the gustatory fibres of the chorda of the tympani follow in proceeding to the nerve centres? Are they represented by the intermediate nerve of Wrisberg? or do they arise from an intra-cranial anastomosis of the facial nerve with a sensory nerve, a branch of the trifacial?

Lussana has no hesitation in adopting the former hypothesis, and he has helped to strengthen it by a number of experiments, in some of which the trifacial was entirely destroyed, the taste remaining uninjured, while, in others, intra-cranial lesions (lesions of central portion) of the facial nerve are accompanied by a change in the sense of taste.

The number of experiments, however, which have produced an entirely opposite result are much more numerous than these. The cases reported by Davaine, Gucneau de Mussy, and Roux, the experiments made by Biffi and Morganti, and Schiff's researches,[1] all seem to prove that lesion of the central portion of the facial nerve produces no effect upon the sense of taste; and that, conse-

[1] See Art. "Goût," in the "Nouveau Dictionnaire de Méd. et de Chirur. Pratiques," Vol. XVI.

quently, the chorda tympani, according to Schiff, consists of borrowed fibres proceeding from the trifacial to the facial nerve, a lesion or entire section of the trifacial, before its division into three branches, producing the same effect on the taste as section of the chorda tympani.

By accepting this conclusion, however, we only place the difficulty a little farther back; for the new question immediately arises, where and how does the facial nerve borrow from the trifacial the sensory fibres which are destined to form the chorda tympani?

Schiff inclines to the belief that in the large petrosal nerve an anastomosis takes place, by means of which the facial nerve borrows from the trifacial the sensory fibres which lead to the tongue. So much controversy is still going on in regard to these results that we refrain from giving the details of the experiments undertaken for the purpose of proving these theories. We will simply sum up in a diagram the theories of Lussana and of Schiff. In

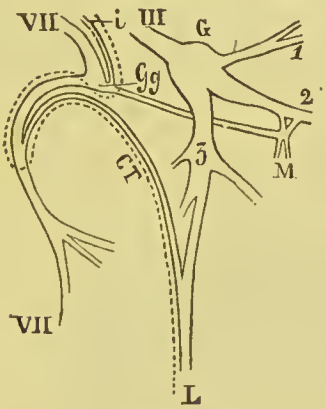


Fig. 105.

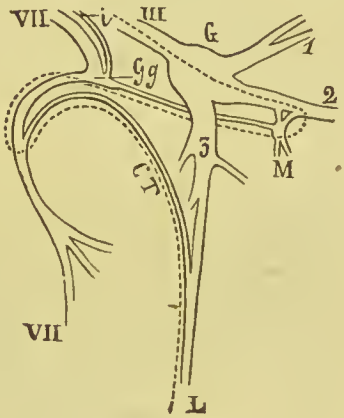


Fig. 106.

the figures 105 and 106, G represents the Gasserian ganglion, developed on the trifacial (III), which then divides into the ophthalmic (1), the superior maxillary (2), and the inferior maxillary (3); L represents the lingual nerve; VII, the facial; *i*, the intermediate nerve of Wrisberg; GT, the chorda tympani; *Gg*, the geniculate ganglion. We see that, in Lussana's hypothesis (Fig. 105), the gustatory fibres, the course of which is represented by a dotted line, pass from the tongue to the nerve centres through the lingual nerve (L), the chorda tympani (CT), the facial nerve, and, finally, through the intermediate nerve of Wrisberg. On the other hand, Schiff maintains that the paths of conduction of the sensory impressions follow the lingual (L, Fig. 107), the chorda tympani (CT), and the facial nerve (VII); but they leave this nerve at the level of the geniculate ganglion (*Gg*), and follow the large petrosal nerve, join the ganglion of Meckel (M), and, consequently, the superior maxillary (2), and, finally, reaches the base of the encephalon by the trunk of the trifacial (III).

We must, however, add that physiologists by no means gener-

ally acknowledge the sensory functions of the chorda tympani. The most recent experiments on this subject are those made by Vulpian, who considers the filaments leading from this nerve to the tongue as similar to those which pass from it to the sub-maxillary gland (Soc. de Biologie, 1873). By exciting these filaments in the corresponding half of the organ, Vulpian produced phenomena similar to those which take place in the sub-maxillary gland during the galvanization of the same nerve; in other words, the tongue grows red and heated on the side galvanized. The chorda tympani is, therefore, a vaso-motor nerve, which here also regulates the dilatation of the vessels (see p. 173). We see in this way how facial paralysis may affect the sense of taste, the function of the lingual mucous being undoubtedly influenced by the vascularization of this tissue.

III. Sense of Smell.

The *sense of smell* is one which gives rise to certain perceptions known as *odors;* it is, however, still more difficult

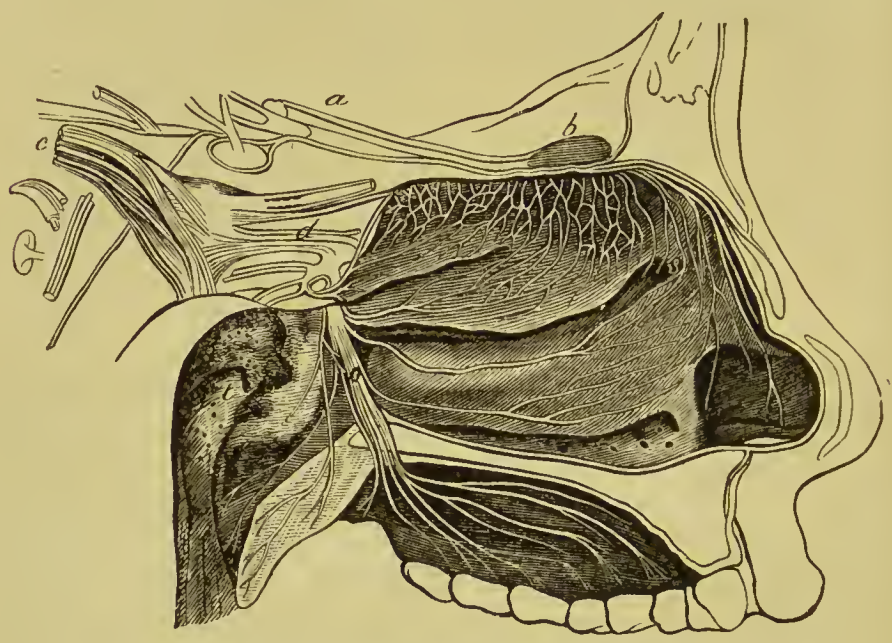


Fig. 107.—External wall of the nasal chambers with the three spongy or turbinated bones and the three meatus.*

to define exactly an *odorous substance*, and the nature of the impressions produced by it, than to define a sapid substance

* *a*, Olfactory nerve. *b*, Olfactory bulb upon the cribiform plate of the ethmoid: below is seen the plexiform disposition of the olfactory branches upon the upper and the middle turbinated bones. *c*, Nerve of the fifth pair, with Gasserian ganglion. *d*, Its palatine branches (upper maxillary and their pituitary filaments.

and its effects. *Smells* cannot be divided into classes, and, setting aside the arbitrary and special appellation of *agreeable* and *disagreeable odors*, we can distinguish them only by the names of the bodies to which they belong.

The sense of *smell* resides in the *nasal chambers* (Fig. 107), but only a small part of this cavity serves for the purpose, the remainder either giving rise to the resonance of the voice (especially the annexed cavities: maxillary, frontal sinus, etc.), or preparing the air inhaled by imparting to it the degree of heat and moisture necessary to the respiratory mucous membrane, as we learned when studying that mucous tissue (p. 286). These parts are formed by three *turbinated* bones, one above the other, which enclose rather narrow *passages* (Fig. 109), the whole being lined with an extremely soft, thick, vascular *mucous*, containing rich venous plexus, and coated with *a columnar epithelium having vibratile cilia;* these latter are also found in the remainder of the conducting tube of the respiratory tree, of which this part of the nasal chambers forms the beginning. In this mucous (Schneiderian membrane) are found numerous glands, which help to keep moist the surface which would otherwise be dried by the movement of the air.

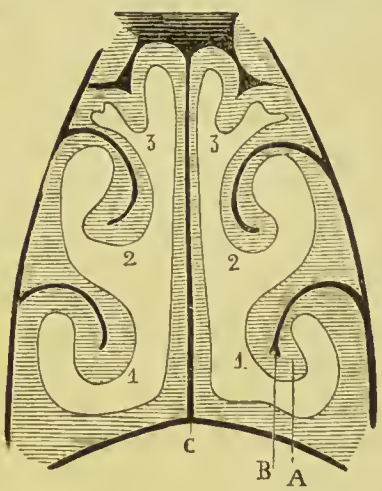


Fig. 108. — Diagram of transverse section of the nasal chambers.*

The sense of *smell* itself appears to be intended as a guard to the purity of the air inhaled: for most substances which are capable of vitiating the air, have some odor, and are naturally under the control of the sense of smell.

The sense of smell resides only in the highest portion of the nasal chambers, in those parts through which the olfactory nerve, the nerve of special sensibility, extends, while the lower parts receive only the branches of the trifacial nerve or the nerves of general sensibility (see *Cranial Nerves*, pp. 35–38). In this region (called the *olfactory region*, of a

* 1, Inferior turbinated bone. 2, Middle turbinated bone. 3, Superior turbinated bone.

A, Thickness of the mucous membrane and soft parts (which are very vascular) with which it is lined. B, Skeleton (bones or cartilages). C, Partition, showing the same parts (mucous membrane and skeleton).

yellow color in animals), the mucous surface changes its nature: here (the upper part of the septum within, and the two superior turbinated without), this membrane is much less vascular, containing fewer glands and no vibratile cilia, but having simply a columnar epithelium; its characteristic feature consists in the terminal branches of the olfactory nerves, these fibres being so fine and so numerous that by their presence alone an experienced histologist will recognize a detached fragment of this *olfactory membrane.* These nerve fibres appear to terminate at the surface by joining the deep and slender extremity of the columnar epithelial cells; at all events, Schultze's researches seem to show that around the epithelial cells of this region are found special organs (*olfactory cells* of Schultze) or fusiform elements, elongated, having a rounded protuberance in the middle with a nucleus, the two extremities being prolonged in fibrillæ. The external prolongation, which is the thicker of the two, passes between the epithelial cells to the free surface, while the internal prolongation appears to continue with the fibres of the olfactory nerve. This appears to be a well-established instance of the relation between the nerves and the epithelium, and it serves to explain the importance of the latter to all the organs of the senses.

The *sense of smell* is exercised either upon *vaporous substances* floating in the air, or imperceptible solid molecules which the air carries along with it; volatile bodies are, therefore, generally odorous. It has been observed that the sense of smell is aided by moisture, and also that flowers are more fragrant in damp weather than in dry. On the other hand, if the quantity of vapor is too great, or if water is introduced into the nasal chambers, the sense of smell is hindered, or even ceases entirely, until the normal condition is restored (the sense of smell is not so acute in foggy weather).

The conditions under which vapors or odorous particles must be brought in contact with the olfactory surface in order to produce the necessary sensation are somewhat peculiar and extremely restricted: they must be brought by a *current of air*, and they can act only while this current is in *motion;* thus, if a piece of camphor is placed in the nose while the air is quite still, no sensation is produced, and the case is the same if the nasal chambers are filled with an extremely fragrant volatile fluid. In order to *smell* perfectly, therefore, we inhale the air by means of short successive inspirations. This is because, in the second place, the *current*

of air must be *slow* and *feeble*. Still more peculiar, however, is it that this *current of air* must be *inhaled*, and must proceed from in front to back, no doubt because it is then broken against the spur which forms the anterior part of the inferior turbinated bone, and thus portions of it rise easily to the olfactory membrane. The air exhaled through the posterior cavity of the nasal chambers produces no impression in passing through, whatever may be the quantity of odorous particles that it may contain; the same is true if, by any artificial means (injection or insufflation), a current of air is directed upon the olfactory mucous, either through the opening of the nostrils, or through a passage made in the frontal and the frontal sinuses. These facts are well known to epicures, who, when they desire to try the flavor of a wine, do not breathe into the nasal chambers through the posterior orifices, but breathe gently forwards and upwards through the orifice of the mouth, and draw in, very slowly and by short jerks, the air which comes in contact with their nostrils.

We have seen that the seat of smell corresponds exactly with the distribution of the *olfactory nerve*, which justifies us in considering this nerve as governing this *special sensation*. Magendie supposed the sense of smell to reside in the trifacial; his reason for this was that, having cut the nerve of the first pair (the olfactory) in a dog, and then held some ammonia to its nose, the animal drew back and shook its head; this, however, as in the case of the tongue, was a phenomenon of general, not of special, sensibility: the caustic vapors of the ammonia acted, not on the sense of smell, but on the sensibility of the Schneiderian membrane in general, which is innervated by the trifacial nerve.

Some clinical observations have, however, thrown some doubts upon the functions of the olfactory nerve, considered as an organ of smell: the most curious of these cases is that of the autopsy of a woman, in whom Cl. Bernard found the bulb and the olfactory trunk entirely wanting, and the corresponding part of the ethmoid bone imperforate; the strict inquiry, however, established the fact that this person's sense of smell had been perfect during life, and that no peculiarity in this respect had ever been observed in regard to her. Instances of this kind cannot be explained, but some experiments seem to confirm the opinion that the olfactory nerve has an office of special sensibility. Schiff took five

young dogs, in four of which he made an intra-cranial section of the first pair, while he cut only the posterior roots of the olfactory branch of the fifth; he found that the latter retained its sense of smell, while the four others lost it entirely.

The sense of smell is much more acute in animals than in man; it serves them as a valuable guide, and is the moving cause in many of their instinctive and deliberate actions: thus connected with the sense of taste it enables them to distinguish the different kinds of food suited to them, and it is the agent of numerous impressions connected with the reproductive functions, etc.[1]

IV. The Sense of Hearing.

Hearing is that sense by means of which we are conscious of the waves of sound produced by the vibration of bodies in the ambient medium (air or water).

The organ of hearing is extremely complicated; in order to understand it we will first examine it in those animals which inhabit the water; in these it is most simple. The essential and fundamental part of the organ of hearing, as found in the inferior fishes, consists of a *small bag full of fluid*, in which nerve fibres terminate in connection with a special epithelium, furnished with prolongations resembling great *cilia*, or small *rods*, that vibrate with every movement of the fluid. The waves of the surrounding medium (fluid) are thus transmitted almost directly to the nerve terminations, and excite these latter. This organ is found in all the higher animals: it consists of the *saccule* or smaller vestibular vesicle and the *utricule* or *common sinus*. With these are connected similar *diverticuli*, consisting of pouches of different forms, but always full of fluid (*endolymph*): these, in the higher classes of fish, are the membranous *semicircular canals;* in reptiles, and especially in birds, there is also a peculiar long and exceedingly complicated canal or tube, which is wound and twisted around itself like a spiral staircase, and is called the *cochlea*. The tube of this cochlea is also divided by a partition called the *spiral plate* (*lamina spiralis ossea*) into two secondary tubes, which communicate with each other at the summit of the organ, while, at the base, one communicates with the rest of the *internal ear* or

[1] See G. Colin, "Physiologie comparée des Animaux." Vol. I. p. 310.

vestibule (*scala vestibuli*), and the other with the *middle ear* or *tympanum* (by the *fenestra ovalis*).

This collection of *membranous pouches* (*utricule* and *saccule*), the *semicircular canals* and the *cochlea*, forms the *internal ear* of the higher vertebrate animals. The *auditory nerve*, or nerve of the eighth pair, terminates here in organs differing apparently in form, but belonging all to the same type, viz., that of organs capable of being set in motion by the vibrations of the fluid in which they are immersed. In the *membranous pouches* (utricule and saccule) these organs consist of epithelial cells in contact with crystals of carbonate of lime (*otoliths*), which strike against them at every oscillation of the fluid; in the semicircular canals (in the *ampullæ*), they consist of epithelial cells furnished with long rigid *cilia*, which are immediately set in motion. The disposition of the cochlea is more complicated; the cochlear branch of the auditory nerve spreads through the spiral membrane (membrana spiralis) in 3000 or 4000 small articulated organs (*organs of Corti*), which cannot here be described,[1] but which, in brief, resemble fragments joined together like the beams of a roof, and swing to and fro with the oscillations of the ambient fluid. The whole of this internal ear or labyrinth arises from a deep vegetation of the integuments of the lateral portion of the head of the embryo; this growth is afterwards more or less separated from the surface from which it sprang. The organ of Corti itself is, therefore, an epidermic production.

The animals which live in the air possess, besides the internal ear, an additional organ, consisting of the middle chamber of the ear or *drum* (*tympanum*). This part, which would be useless in water animals, for whom the waves of sound are communicated readily from the ambient fluid to the fluid of the labyrinth, is necessary to facilitate the communication of the waves of a gaseous medium to the fluid medium of the organ; thus we know that sounds do not pass readily from the air into water. The *middle chamber of the ear* resembles a drum hollowed out in the petrosal substance and contains an organ of conduction intended to facilitate the transmission of waves of sound (Fig. 110); it consists of a more or less regular bony chain, leading from the internal ear (*fenestra ovalis*) to the *membrana tympani;* this latter

[1] See Lœwenberg, "La Lame spirale du Limaçon." ("Journ. de l'Anat. et de la Physiol." 1866.)

membrane comes in direct contact with the external air, although it is placed at one end of a collecting and concentrating apparatus (composed of the *pinna* or auricle of the ear and of the external auditory canal). We can best understand this by reducing the *internal ear* to a drop of liquid, and supposing a vibrating membrane (membrane of the *fenestra ovalis* and the base of the *stapes*) which vibrates by the intermediation of a solid chain, the *chain of the ossicles*, the other extremity of which is connected with a collecting organ, the *membrana tympani*, and the cavity of the concha. As the second membrane (the deepest, the fenestra ovalis) is



Fig. 109.—Diagram of the auditory apparatus in man.*

much smaller than the first (membrane of the tympanum or drum), the slightest vibration of the latter will set in action the former. We will now proceed to study the office of these parts, taking them in an opposite direction or from without inwards, which is the direction which the waves of sound follow.

A. *External ear.*

The *pinna of the ear or concha* is an organ which has little sensibility of its own, and whose general and tactile sensibility is somewhat dull; the ornaments with which, even among civil-

* From right to left are seen the external ear, the auditory passage, the tympanum with the chain of small bones, the Eustachian tube, and the labyrinth. (Dalton, "Human Physiology.")

ized nations, it is often weighed down, scarcely excite any sensibility in it. It is essentially composed of a cartilage, folded in a peculiar manner, which appears to constitute it an organ for *collection;* both its direction and its form are changed in animals by the action of intrinsic and extrinsic muscles, which are brought into play according to the degree of attention with which the animal listens to different sounds. In man, these muscles are rudimentary, or, at the most, only the extrinsic muscles contract with the fronto-occipital system, when the attention to any sound is carried to its highest degree.

This pinna is thus of little service for intensifying sounds, and those who are deprived of it do not experience any sensible change in their power of hearing. It appears, however, to be of use in enabling us to judge of the *direction* of sounds: a person deprived of it, or who, for the sake of experiment, renders it useless by flattening it forcibly against the head, or by filling its convolutions with wax, will find himself unable to distinguish the direction from which sounds proceed; there is no doubt that we judge of the direction and origin of sounds by the slight modifications in their intensity produced by the manner in which the sound-waves strike the pinna, and are reflected from it. We judge of their *direction*, also, by the fact that the sound *does not strike both ears alike:* it rarely happens that we can distinguish whether a sound proceeds from directly before us, or directly behind us; we therefore turn the head slightly, and incline the ear in the direction from which we suppose the sound to come.

The *external auditory canal* (*meatus auditorius externus*) is of greater importance; if this is obstructed, the sense of hearing is diminished, and, if it is too much contracted, deafness sometimes follows.[1] It furnishes two methods by which *sounds may be transmitted:* these consist of the *column of air* inside it, and the *cartilaginous* and *bony walls* of which it is formed; these walls transmit the waves by vibration, directly to the bones of the head, and thence to the fluid of the labyrinth, and we can see how much easier the transmission must take place, since the vibrations spread through solid mediums. This auditory canal is also remarkable for its peculiar sensibility: at its opening are found large hairs, and if these are touched, or any excitation brought to bear

[1] See P. Bonnafont, "Traité des Maladies de l'Oreille." 1873, p. 120.

a little below them, strange and unexpected reflex phenomena will follow, such as a feeling of nausea, or of uneasiness and general discomfort, which warns us of the danger to which the organ of hearing is exposed; these are, in short, phenomena of general sensibility, and have no connection with the sense of touch. In this canal (in its cartilaginous and fibrous portion) are found the *ceruminous glands;* we examined the secretion of these glands, when studying the functions of the skin, and found it the thickest and most sticky of the secretions of perspiration: this cerumen serves to prevent any substance from reaching the bottom of the external auditory canal, where its presence would be injurious to the membrana tympani.

B. *Middle chamber of the ear.*

The *membrana tympani* is formed of connective and elastic fibres, and contains a large number of vessels; here, as in the case of the pinna of the ear, the abundance of the vessels appears to be intended for the purpose of keeping up the temperature of these parts which are always uncovered and exposed to that air from which they receive vibrations. The membrana tympani is essentially a collecting organ; it is situated at the bottom of the external auditory canal, but does not share in the peculiar sensibility of the latter: if an insect penetrates so far as to touch it, no reflex phenomenon is produced, but only a sensation resembling that accompanying a sound, and which is caused by the vibrations communicated to it. It is, therefore, simply a physical organ, for the reception of air, or of the sonorous vibrations from the walls of the canal.

This membrane is not normally so situated as to collect the waves of sound, but appears, on the contrary, to avoid them up to a certain point, being *oblique* from top to bottom and from back to front; it seems, in short, to continue the supero-posterior wall of the canal; the younger the subject the more decided the obliquity, while in the *fœtus* this membrane is nearly *horizontal.* It is not a plane, but consists of a very low *cone*, having its internal summit slightly flattened, and its edges attached to the deep opening of the external auditory canal; it is enclosed in a sort of frame which appears distinctly in the form of an imperfect ring in young subjects. This membrane is, therefore, *convex on the interior*, its convexity being preserved by a chain of small bones, a portion of which (the *handle* of the *malleus*) is contained in the thick

part of the membrane, making it incline inwards (Fig. 110): this convexity or tension is produced, either by variations in pressure in the air in the drum, or by the action of a muscle (*internal muscle of the malleus*). If from any cause the air of the drum becomes rarefied, the exterior air presses upon the membrane, forcing it deeper into the cavity of the tympanum, and, consequently, stretching it while increasing its convexity (in the direction indicated by the arrows in Fig. 110). The *internal muscle of the malleus* (*tensor tympani*) produces the same effect: it draws inwards the handle of the bone, and consequently the membrane, increasing the convexity and the tension of the latter.[1] This is the only muscle whose *action* or *existence* has been satisfactorily demonstrated; either the other so-called muscles of the internal chamber of the ear have no existence (anterior and external muscles of the malleus), or their action is not yet perfectly understood (muscle of the stapes, *stapedius*), at all events they do not produce the effect of relaxing the membrane, which, by means of its elasticity, returns of itself to the position of repose directly its tensor muscle ceases to contract.



Fig. 110.—Membrane of the tympanum and ossicles.*

The purpose of this temporary tension of the membrane is now easily understood. Bichat supposed that the tension of the membrane must be increased in order to increase the power of the sound; this hypothesis is, however, contrary to the laws of physics, and Savart has shown that the tension

[1] Some persons possess the power of contracting the musculus tensor tympani at will, and thus stretching the membrane of the tympanum. This tension is manifested by a slight cracking sound, which is produced in the ear at each contraction of the muscle: the movements made by the membrane under the influence of these voluntary contractions may also be observed by the aid of the speculum. Nearly all those physiologists whose attention has been directed to this circumstance, and who have attempted to produce this contraction, have succeeded with the greatest ease: Bérard, Müller, and Wollaston are especially mentioned as having done so. (Bonnafont, *op. cit.*, p. 270.)

* *a a*, Membrane of the tympanum. *b*, The malleus. *c*, The incus. *d*, The stapes.

of the membrane serves to diminish the effect of the sound upon it (as the more a membrane is stretched, the less *full* will be the vibrations), and to soften certain disagreeable sounds. On the other hand, this tension makes the membrane vibrate more readily to acute sounds; and to hear these demands very close attention (the greater the tension of a membrane, the more *numerous* its vibrations).

Next to the membrane of the tympanum comes the *chain of small bones*, connecting it with the membrane of the oval fenestra (base of the stapes). In the inferior animals, this chain simply consists of a straight and rigid stalk (as found in some anourous amphibians, the *pipa*, for instance); in frogs it takes the form of a broken line, a small bone, long and curved, and which is called the *columella;* in man, finally, it is formed by the junction of three small bones or ossicles (the malleus or hammer, the incus or anvil, and the stapes): these bones are articulated, but, in regard to the transmission of sound, they may be considered as anchylosed, it having been proved that these articulations do not directly operate for the transmission of sounds.

The chain of ossicles through which the sound waves chiefly pass, crosses a drum filled with air, called the tympanic cavity; it is flattened from without inwards, and, like the membrana tympani, exhibits a plane oblique to the external auditory canal. It is supposed that the sound waves are not only transmitted by this jointed connecting-rod of bones, but that the air in the drum also serves to convey them to the *fenestra rotunda;* this is possible, but not very probable, and at all events, this mode of progression must be only secondary, for the round fenestra avoids the sound waves, as it were, being hidden beneath the *promontory* (tuber cochleæ, or projection outwards of the first turn of the cochlea directly opposite the protuberance of the membrana tympani); the correspondence of this round fenestra with one of the openings of the cochlea, which communicates on the other side with the vestibule, appears to be intended for the purpose of giving free play to the fluid waves which pass through this complicated organ. Finally, since sound is more readily transmitted through solids than through fluids, the chain of small bones must have a much more important office to fulfil than the air, which latter, no doubt, serves only as an insulating apparatus. The membrana tympani, and these ossicles, with the exception of the stapes, may be destroyed without the complete abolition of hearing; it will only be more

or less obstructed. The loss of the stapes is much more serious, and, according to Bonnafont, always causes deafness. This fact is easily explained: the stapes is attached at its base to the *oval fenestra*, closing it entirely, and is so firmly fastened to it that it cannot be removed without tearing the membrane of the oval fenestra, and thus allowing the endolymph or liquid in the internal ear to flow out; it is not, therefore, properly speaking, the loss of the bone which occasions deafness, but rather the escape of the fluid through the aperture made by the ablation (Bonnafont, *op. cit.*, p. 264).

Two organs are attached to the middle chamber of the ear: these are, behind, the *mastoid cells*, which are irregular cavities, or sinuses hollowed out in the mastoid process of the temporal bone; and, in front, the *Eustachian tube*, connecting the drum of the tympanum with the nasal part of the pharynx.

The *mastoid cells*, being full of air, are generally considered as a resonant organ; this supposition has, however, no other ground than the fact that the air in the drum vibrates, and, consequently, its vibrations are intensified by those of the air in the mastoid cells. We have just seen that the vibrations of the air in the drum are of no importance whatever; neither have diseases of the mastoid cells furnished any indication as to the purpose of these cavities. We incline to the opinion that the mastoid cavities are empty spaces, having no special function, and intended only to increase the size of the cavity of the tympanum. We shall presently see that in the normal state the tympanum is closed on all sides: now, as the tympanum is an extremely small cavity, any sudden change in the tension of this thin layer of air which covers the inner surface of the membrana tympani would, no doubt, have an injurious effect upon this membrane; this effect would be mitigated by the addition of another cavity, adding its capacity to that of the tympanum properly so called; thus those animals which are exposed to sudden and considerable changes of atmospheric pressure, as birds which fly very high, have their mastoid cells more fully developed than is the case with other animals, these cells even communicating with other supernumerary bony cavities.

The *Eustachian tube*, which is situated in front of the middle chamber of the ear, that is, facing the mastoid cells, is a long tube extending from the tympanic chamber to the pharynx, and thus forming a means of communication be-

tween these two cavities. Many suggestions have been made as to the probable use of this tube: some have supposed that it is intended to enable us to hear our own voice; the bones of the head, however, serve to propagate this sound, and besides, in its normal condition, the tube is closed; if, by any cause, it is opened for any length of time, the person hears, not only his own voice, but every sound produced in the upper part of the body, such as the sound of the breathing, the movements of the velum of the palate, of the tongue, etc.; it has been observed, in some cases of this kind, that patients whose attention was thus constantly directed to the various phenomena of the organism have at length become hypochondriacs, an effect which is generally produced by paying too much attention to the facts of our own internal organic existence (see p. 56).

The Eustachian tube is then normally closed by means of the juxtaposition of its walls, and opens only when some special organ separates these, by acting on the membranous and movable *outer wall*, and drawing it away from the other, which is cartilaginous and quite stationary. This office is performed by the *circumflexus* or *tensor palati*, or muscle of the velum of the palate, and the effect of the opening thus made is to bring the air of the drum into communication with that of the nasal chambers, that is to say, the external air. The muscles of the velum of the palate, however, contract only during the movements of deglutition; the act of swallowing cannot take place when there is nothing to swallow, and requires, at least, a few drops of saliva. We return, therefore, to what we have already said on the subject of salivation and deglutition, when we pointed out that the first of these functions is closely connected with the normal operation of the sense of hearing; and also observed that the secretion of the saliva, which is almost useless in the carnivorous animals, as regards digestion, is chiefly connected with the intermittent movements of deglutition, which may be compared to the winking of the eyes and are intended to effect the opening of the Eustachian tube (see pp. 222 and 226). This is why we make similar movements of deglutition, even when asleep, and especially in ascending great heights, because, beside the variations in the exterior air which render a restoration of equilibrium necessary, the gaseous exchanges of the blood have the effect of varying the tension of the interior air; these exchanges are sometimes very sudden and of considerable

amount, as we saw in regard to the stomach and the digestive tract. In our study of deglutition we made use of this special and intermittent working of the Eustachian tube for the purpose of demonstrating the strict occlusion of the naso-pharyngeal orifice; and then observed that the hearing is obstructed (on account of the rarefaction of the air in the tympanic cavity), if one or more deglutitions are performed with the nostrils closed; and showed the necessity of deglutition performed with the nostrils open in order to restore the sense of hearing to its natural state (see p. 226).

The tympanic cavity is crossed by a nerve (the *chorda tympani*) which leads to the salivary glands, and whose function consists of exciting the secretion of saliva; so certain sounds, especially sharp ones, cause an abundant secretion of saliva, no doubt by means of their action on the chorda tympani through the medium of the membrane against which its nerve fibres are applied; at all events, we cannot avoid associating this anatomical fact of the passage of the nerve of the salivary secretion in the cavity of the tympanum, with the physiological fact which we have just been studying, namely, the essential connection between the secretion of the saliva and deglutition with the opening of the Eustachian tube, and, consequently, with the keeping up of the normal pressure in the cavity of the tympanum. This relation between the middle chamber of the ear and the pharynx is made plain by the study of embryology: in the fœtus these parts are confounded together in the first pharyngeal cleft, and the Eustachian tube is the remnant of this fœtal communication (see p. 405, *Physiology of the Chorda Tympani*).

C. *Internal ear.*

The vibrations reach the fluid of the labyrinth either through the *columella cochleæ* (chain of small bones), this being the usual means of communication, or by the bones of the head, especially the walls of the external and the middle ear; the latter is the case with persons who, although they have lost the chain of small bones, are yet not completely deaf. The fluid of the labyrinth then communicates these vibrations to the various terminal organs of the auditory nerve which are situated in the vestibular sacks (utricula and saccula), in the semicircular canals (ampullæ and crest), and in the cochlea (spiral lamina with the organ of Corti). Nothing, however, is yet positively known as to

the functions of these various parts of the internal ear. It has been remarked that the cochlea appears to be necessary to animals that hear by means of vibrations of air, and that, on the other hand, a sonorous larynx, which is capable of emitting musical sounds, is generally found to exist with it, while also accompanied by a sensibility in the animal to musical sounds: it thus appears to be the chief organ of *musical perception*, and the calculation which has been made of the number of elements in the organ of Corti, compared with the scale of musical notes, seems to confirm this view. It has also been suggested that the vestibular chamber may possess the power of judging more especially of the *intensity* of notes, and even of *sounds*, and that the three semicircular canals may, by means of their triple arrangement of position, horizontal and transverse, vertical and longitudinal, and horizontal, have the faculty of judging of the *direction* of sounds; we have, however, already seen that the pinna of the ear has also the property of defining the direction of sounds.

Whatever be the special function of each part of the internal ear, the shock upon the terminal organs of the nerves always enables us to distinguish several special conditions in the sound waves, which the science of physics shows to be the cause of the *difference* in sounds. The *fulness* of these vibrations is what constitutes the *force* or *intensity* of sounds, while their *rapidity*, or number in a certain space of time, constitutes the *acuteness* or *gravity* of sounds, and enables us to distinguish the sounds in a perfect scale from the lowest (32 vibrations in a second) up to the highest (76,000 vibrations in a second). Finally, we distinguish in sounds a special quality called their *tone;* this is more difficult to define, but appears to consist of the sound resulting from the combination of several notes, whose *tone* is different, according to the varieties of the combination. (See *Phonation*, p. 359.) Habit certainly enables us to judge of the nature of the vibrating body by its tone, which constitutes what might be called, in a physiological point of view, the *savour* of a sound; by this we recognize the voice of a person, judge of the sex by the voice, and even judge of the sentiments of the speaker; in all these cases, although the sounds may be of the same *intensity* and *pitch*, they are produced by different combinations of the same simple sounds; the waves produced have, therefore, a different form, and in judging of the *tone* of a note, we may be said to judge of the *form of the vibra-*

tions. No doubt this faculty which the organ of hearing possesses for judging of such different qualities (*fulness*, *rapidity*, and *form*, or *combinations* of the sound waves), renders necessary that remarkable complication of structure in the internal ear which will long continue to baffle physiologists. According to Flourens, the *semicircular canals* have great influence on the *equilibration* of the animal. This physiologist discovered that injury to these canals produces *rotatory* movements. Vulpian has made similar experiments on a pigeon, and shown that rotatory, rolling, or falling movements are produced, according as the horizontal canal, the anterior vertical canal, or the posterior vertical canal is destroyed. These effects are, however, caused rather by a vertigo, and are no proof that the semicircular canals govern the equilibrium and the co-ordination of movements. It may be asked, finally, whether the phenomena observed in these experiments are really owing to lesions of the semicircular canals, and not to that of the adjacent parts. Böttcher made the experiment of carefully detaching the semicircular canals in a frog, and succeeded in destroying them without injuring any other part of the labyrinth or of the encephalon, and he never found in the batrachians this operation followed by any difficulty in walking or standing. This effect is produced only when the lesion is deep-seated. We may conclude from this that the semicircular canals really form an organ of hearing, and not an organ which governs the equilibrium of walking and standing. (Böttcher, "Medic. Zeitschr.," 1872.)

V. The Sense of Sight.

The sense of sight enables us to judge of the *luminous properties* of the objects by which we are surrounded, and, consequently, of their *color*, their *form*, and their *position.* The organ of sight (the *eye*) is essentially composed, 1, of a membrane (the *retina*), connected with the nerve terminations, and upon which the impressions of the luminous rays are made; 2, of a *dioptrical organ* intended to collect and condense the rays of light upon the membrane just mentioned, where they represent in miniature external objects, as on a screen in a dark room; 3, of *membranes*, *attached* to these two organs, for the purpose of securing and modifying their functions. These different parts (Fig. 112) are connected like the other organs of the senses, in a physiological point of view, with the study of the surfaces of the organism,

which (with the exception of the nervous portions) are formed in a great measure in the embryo, by deep and extremely complicated growths of the external integument. To the

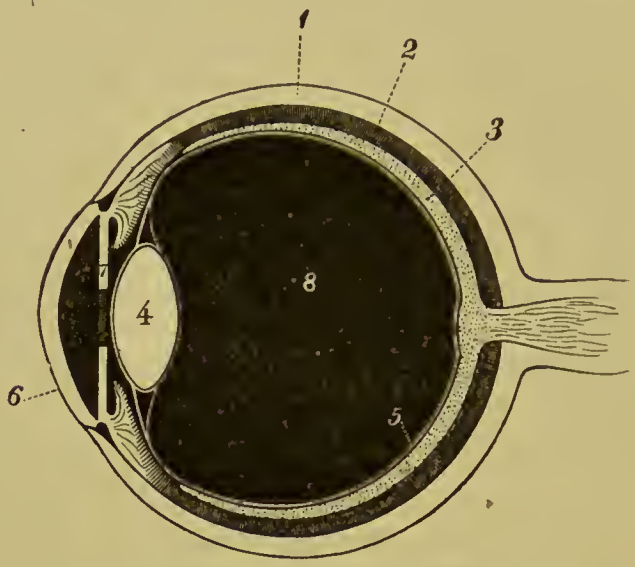


Fig. 111. — The globe of the eye (vertical section).*

eyeball or globe of the eye thus constituted, accessory organs are attached, intended either to move it (muscles of the eye), or to protect it from external injury (eyelids and lachrymal system).

We shall successively consider: —

1. Physical dioptric apparatus.
2. Accessory membranes which maintain and modify its function.
3. Sensitive membrane or *retina.*
4. Appendages of the eye.

1. The *dioptrical apparatus.*

A. *Media of the Eye.*—The dioptrical apparatus consists of all the transparent media through which the rays of light pass in order to reach the sensitive membrane situated at the bottom, or fundus, of the eye; these are, beginning in front, the *cornea*, the *aqueous humor*, the *crystalline lens*, and the *vitreous humor;* the cornea, which, in an anatomical point of view, forms a part of the covering of the eye, in a physiological point of view constitutes one of these media.

* 1, Sclerotic. 2, Choroid. 3, Retina. 4, Crystalline lens. 5, Hyaloid membrane. 6, Cornea. 7, Iris. 8, Vitreous body. (J. C. Dalton, "Human Physiology.")

The *transparent cornea* is formed of a *basement membrane* of collagenous tissue (see Fig. 23, p. 96), covered, both in front and behind, with an epithelial layer; that of the posterior surface is simple (*membrane of Demours* or *of Descemet*); that of the anterior surface resembles the epithelium of the conjunctival mucous layer, which is itself continuous with the skin and the epidermis; thus superficial diseases of the cornea are closely connected with diseases of the skin or epidermis. The aqueous or *watery humor* is contained in the *anterior chamber* (where we shall presently study an appendage of the choroid, called the *iris*), between the posterior surface of the cornea, and the anterior surface of the crystalline lens; this fluid closely resembles water, containing in solution a small quantity of albumen and salts, and is secreted by the *membrane of Demours* (*membrane of the aqueous humor*).

The *crystalline* lens consists of an exterior membrane, called the *capsule of the crystalline lens*, and an inner substance, called the *body of the crystalline*. The *capsule* is an amorphous and very elastic tissue; if an incision is made into its substance, it retracts and expels its contents (as in the operation for cataract); its whole inner surface is covered with cells, from which the contents, or body of the crystalline lens may be reproduced. This *body*, indeed, is formed of prismatic elements, arranged regularly in concentric layers (Fig. 112), and which are produced by the metamorphosis of cells; the study of embryology shows the germ from which the crystalline proceeds to be an offshoot from the epidermis (Fig. 113), which, finally, becomes detached and remains alone in the centre of the eyeball or ocular globe. The layer of cells lining the inner surface of the capsule thus corresponds to the layer of Malpighi in the skin: the crystalline lens is developed by means of this layer, in which are constantly found the zones of young cells in the course of transformation into prisms.



Fig. 112. — Disposition of the fibres of the lens.*

* This figure shows the regular disposition of the prisms of the crystalline lens, the extremities of which are joined together on both surfaces, the point at which they meet forming a sort of three-cornered star; thus a lens which has been hardened, either by the effect of heat or of chemical reagents, generally cracks in this stellate form, corresponding with the lines shown above.

The *vitreous humor* or *hyaloid membrane* is composed of collagenous tissue, and resembles the gelatine of Wharton, especially in young subjects; it is contained in a very thin and transparent sack, called the *hyaloid membrane.*

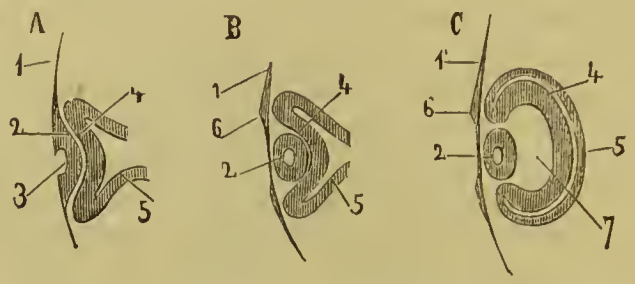


Fig. 113. — Development of the crystalline lens (Remak).*

B. *Refraction.* — This group of media forms, in a physical point of view, a series of *three lenses, differing greatly from each other: the first, consisting of the cornea and the aqueous humor*, is a *convexo-concave lens*, and is extremely complicated on account of the various layers of which the cornea is composed. The *second*, or *crystalline*, is a *bi-convex* lens, the anterior surface of which is more curved than the back; this, too, is very complicated, its concentric layers increasing in density from the periphery to the centre. Finally, in the third place, the vitreous body consists of a *concavo-convex* lens, being hollowed out in front for the reception of the crystalline lens. Immediately behind this latter lens is found a membrane which is sensitive to light and which is called the *retina.*

Let us suppose for the sake of simplicity that, instead of these three lenses, we have a single lens of the same total converging power, and we shall then easily understand the final result of the progress of the rays of light. The whole system, in short, may be represented by a lens formed of a substance whose index of refraction is from 1.39 to 1.40, and whose focal distance is 17 mm., 0.48. The luminous rays, from a given point outside, diverge as they fall upon the

* A, B, C mark the different degrees of *invagination* or separation of the pouch from which the crystalline lens is formed. 1, Epidermic fold. 2, Thickening of this fold, pouch of the separated crystalline (at B). 3, Crystalline *fossette*, which will afterwards appear as the centre of the lens. 4, Primitive ocular vesicle (nerve pouch arising from the encephalic centre), the forepart of which has a depression for the lens. 7, Cavity formed by the compression of the ocular vesicle, and which is to be occupied by the vitreous body. 6, Point at which the lens is detached from the epidermic fold.

cornea, converging again after passing through this dioptrical organ, and uniting in a point which, in the normal state, and under circumstances which we will mention, is situated directly on the retina: it is here that external objects are represented in smaller dimensions. If the convergence, however, does not take place exactly on the retina, but rather in front or behind it, we can easily understand that every *point* of the object presented to the eye will be represented on the membrane, *not as a point, but as a small circle*, which corresponds to the plan of section by the retina of the converging cone, which these rays form before their union, or of the diverging cone which they form after their union (Fig. 114).

In order to make this perfectly plain, let us give the name of *objective cone* to the cone of luminous rays which, proceeding from the luminous point, diverge as they fall upon

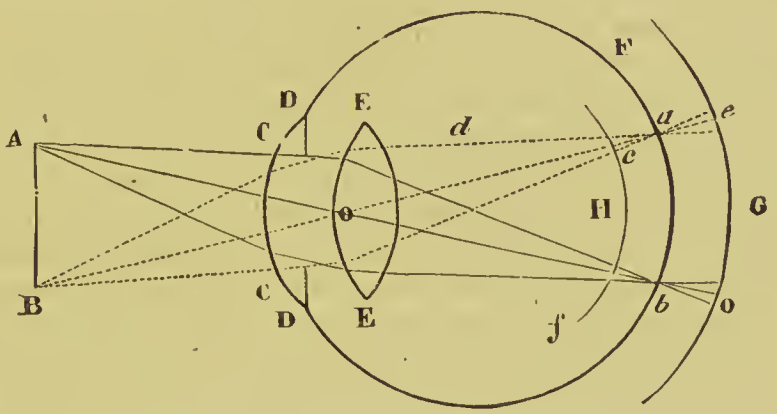


Fig. 114. — Ocular and objective cones.*

the cornea, and that of *ocular cone* to the cone which represents these rays after undergoing the converging influence of the ocular lens (Fig. 114): the slightest familiarity with optics will show us that if the rays of light come to us from a great distance, as from a star, the *objective cone* will attain

* A, B, The luminous points under consideration. *c*, *c*, Cornea. D D, Iris. E E, Lens.

At first the luminous rays which set out from the points A or B are bent by the cornea C C and by the watery humor contained between this membrane and the crystalline, that is, they are brought near to the median ray which travels on a line parallel with the axis. A second refraction takes place in the lens, and the final result appears in the form of ocular cones, the summit of which is at *a* and *b*, or exactly on the retina: but we also see that if the retina, instead of exactly corresponding with the summit of the ocular cones, intersected them either farther forward (at H) or backward (at G), the image formed upon this membrane would no longer be a point, but a small circle (*circle of diffusion*).

its greatest length, while the *ocular cone* will become as short as it is possible for it to be. If, on the other hand, the luminous rays proceed from an object very near the eye, the *objective cone* will be very short, while the *ocular cone* which it produces in the eye will be much longer than in the former case. We see, therefore, that it is only when at a certain distance from the luminous object that the ocular cone is of such a length that its summit falls exactly on the retina; in all other cases, the luminous point being farther from, or nearer to, the eye, the ocular cone produced will be either too long or too short, and its summit will consequently be either before or behind the retina: in short, the luminous point will be represented on the retina, not as a point, but as a small circle, called the *circle of diffusion*, and the image resulting from it will be confused.

What would happen in a physical organ such as we have described does not, however, take place in the eye, in its normal state. Whatever (within certain limits) be the distance of the luminous point, we have the power of bringing the summit of the ocular cone produced by the rays of light proceeding from it, directly upon the retina: a man can alternately look at, and see with nearly equal distinctness, a star and the end of his nose. In short, we have the power of *adapting* or accommodating our eye to different distances.

C. *Adaptation or Accommodation.* — The method of *adaptation* or the *exact coincidence of the summit of the ocular cone with the retina*, has been only recently and exactly defined. For a long time the existence of this accommodation was denied. It may, however, be proved in several ways. If, for instance, we hold up two fingers, one behind the other, at a certain distance, and fix our attention on one, we shall find that we see distinctly only this one, the eye being *adapted* to see only one and not the other, which appears vaguely defined; this is because, at this moment, one of the two fingers is distinctly painted on the retina, while the other only produces *circles of diffusion* upon it. This fact is still more clearly demonstrated by a celebrated experiment made by Scheiner, and which consists in placing before the eye a card in which two small holes are pierced near each other (Mm Nn, Fig. 115), and then looking through them at two luminous points (the heads of two pins, for instance) placed one before the other, at a certain distance (as with the two fingers in the foregoing experiment): *if we look at one of these points fixedly, we shall see the latter double.* The reason of this is owing to

the fact that, when we look at the luminous point *a*, through the two openings Mm and Nn (Fig. 115), a phenomenon of adaptation takes place in the eye, by means of which the summit of the ocular cone falls upon the retina; the summits of the two partial cones passing through the two openings are joined together in one (in *a*), these two cones making a part of the total cone which would be produced if the luminous point were looked at with the naked eye; this is the case,

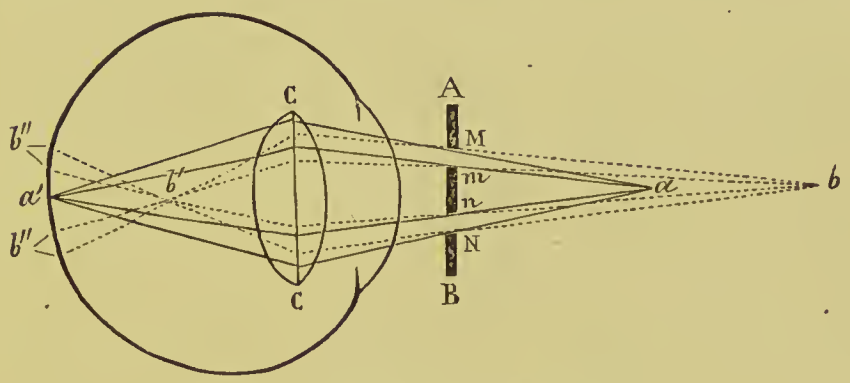


Fig. 115. — Experiment by Scheiner.*

however, only with regard to the point *a*; the objective cone of the point *b*, being longer, its ocular cone will be shorter; and the summit, consequently, will be in front of the retina, and can strike this membrane only by diverging after bringing about the intersection of its rays: if then, as in this experiment, the cone be divided in two by looking through two holes, the object *b*, which is not looked at, will be projected as *two distinct cones* (and will be seen *double*); since they strike the retina, not at the point of their common summit (*b'*), but farther back, where they are again separated (*b''*, *b''*). The eye, in this case, is evidently so adapted as to see *a* and not *b*: but if *b* be looked at attentively, *a*, in its turn, will appear double.

These facts are sufficient to prove that we possess the power of adapting or accommodating our sight to different distances, and this is true up to a certain point, whatever be the distance; thus we can see objects which are placed at an

* A B, Diaphragm with two apertures (Mm and Nn).

a, Point for which the eye is adapted, and the image of which appears at *a* (on the retina).

b, Point for which the eye is not adapted; the luminous rays proceeding from it meet at *b'* (in front of the retina), diverge again, and meet the retina at *b'' b''*, causing the point *b* to appear double.

indefinite distance, and can see clearly those at a distance of 25 centimetres. This is the distance, in fact, at which we receive the greatest quantity of light, and the faculty of adaptation usually lies between an indefinite distance and one of 25 centimetres.

There are, however, sometimes, great differences in this phenomenon; the limits which we have mentioned are those

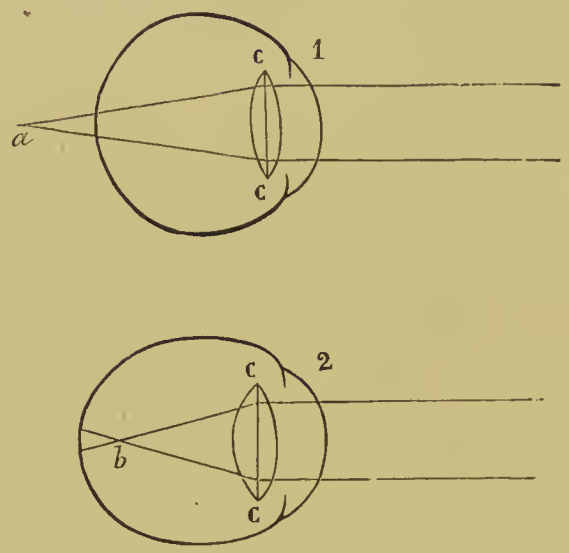


Fig. 116. — Hypermetropic eye and myopic eye (far-sighted and near-sighted eye).*

belonging to eyes in the normal condition, which are called *emmetropic*. The ocular media of some persons, however, have so little converging power that, whatever be the length of the objective cone, the ocular cone is never sufficiently short to allow its summit to fall upon the retina; even when the luminous point is at an infinite distance, its image goes beyond the retina; such persons are called *hypermetropic*, in other words, the object would have to be placed at distance more than infinite before the summit of its ocular cone could

* 1, *Hypermetropic Eye.* — The luminous rays ariving from an infinite distance (parallels) produce an ocular cone, the summit of which falls beyond the retina (at *a*), either because the cone is too long (lack of converging power in the media of the eye), or because the retina is too far forward (the eye being too short).

2, *Myopic Eye.* — The luminous rays from an infinite distance (parallels) produce an ocular cone, the summit of which falls in front of the retina (at *b*), either because this cone is too short (excess of converging power in the media), or because the retina is placed too far back (the eye being too long). Donders's researches seem to show that short-sightedness is owing to this latter cause, as is well shown in the figure: the ocular globe being greatly elongated from back to front).

fall upon the retina (Fig. 116, 1): such eyes are called *hypermetropic*, and this want of convergence (or shortness of the ocular cone) constitutes *hypermetropia*. On the other hand, the ocular medium of some persons has so much converging power that the ocular cone is always too short, and, in order to see objects distinctly, they are obliged to place them very near the eye; so that, as the cone lengthens, its summit may fall upon the sensitive membrane: this is the case with *short-sighted* persons (Fig. 116, 2), and this shortness of the ocular cone constitutes what is called *myopia*.[1]

We see that *hypermetropia* and *myopia* are two opposite conditions; in the former, the eye, when in the state of repose, and making no effort to adapt itself to objects, sees only those which are at the greatest possible distance from it; while in the latter, under similar circumstances, it sees those only which are close at hand. Another condition of the eye which is frequently mistaken for *hypermetropia* is that called *presbyopia;* this derangement of the functions of the ocular medium consists in a diminution of the power of adaptation which can be no longer exercised on objects near the eye; this is generally found to be the case as persons advance in age. In *hypermetropia* the ocular cone is always *too long;* in *myopia*, it is always too short; in both cases, however, the power exists of modifying the cone, by adaptation, especially of shortening it, as we shall presently see. A *far-sighted* person, on the contrary, or one suffering from *presbyopia*, has scarcely any power of modifying the cone in order to see objects near the eye; thus we see that if a normal eye may become *presbyopic*, a *hypermetropic* or a *short-sighted* eye may do so likewise, and that short-sightedness and presbyobia may exist together.

Means of remedying these defects of sight have, however, been found in optics: for the purpose of modifying an ocular cone which is too long or short, either a concave or a convex glass is placed before the eye. If we have the slightest knowledge of physics, we shall be able to understand that a concave or diverging glass, lengthens the ocular cone by diminishing the converging power of the eye: *short-sighted* persons, for this reason, use *concave glasses*. On the other hand, a convex or converging glass shortens the ocular cone

[1] See, in the "Nouv. Dict. de Méd. et de Chirur. Prat.," articles by Liebreich and Javal: "Accommodation, Emmétropie, Diplopie, Asthénopie," etc.

by increasing the converging power of the eye: *hypermetropics*, therefore, make use of a *convex glass*, for the purpose of shortening the ocular cone, as do also far-sighted persons when they desire to see objects near at hand, their power of accommodation or adaptation being insufficient for this purpose.

The study of these various degrees of converging power in the eye, and of the artificial means by which its defects are remedied, will enable us to understand how accommodation is effected in the normal condition. The use of glasses, of which we have just spoken, is a sort of artificial accommodation, especially in the case of far-sighted persons. It is, therefore, probable, that in physiological accommodation, something similar takes place; in other words, the converging power of this organ is modified.

It was for a long time supposed that the mechanism of accommodation consisted in a change in the form of the eye, modifying, not the ocular cone, but the position of the retina; which would then be placed at the summit of the cone, causing the eye, when looking at objects at a distance, to shorten in antero-posterior diameter under the influence of the recti muscles of the eye, and to lengthen under that of its oblique muscles, when looking at objects close at hand. This function of the motor muscles of the eye is, however, entirely hypothetical, and the theory is contradicted by the anatomical arrangement of these muscles, as well as by physiological experiments.

It has been also supposed that the crystalline lens can be moved backwards or forwards, and can act in the same manner as we use the objective in a microscope when we desire to bring an object into focus; a knowledge of anatomy, however, shows that this is impossible, and direct experiments have shown that there is no foundation for such a theory.

Direct experiment shows that accommodation, as our study of artificial adaptation would lead us to suppose, *consists in a change of curve, and, consequently, a change in the converging power of one only of the media of the eye, the crystalline lens.* The experiment is made by studying the images furnished by the different surfaces of the media of the eye, these surfaces acting like mirrors. Thus we may easily observe that objects are reflected in the surface of the cornea, as well as in the anterior and posterior surfaces of the crystalline lens; so that, if we place a light before an eye (Fig. 117), we shall find in the eye three images of the flame: *the two*

upright ones (*a* and *b*) appearing in the cornea (*a*), and in the anterior surface of the crystalline lens (*b*) (convex mirrors); and the one *upside down* (*c*), on the posterior surface of the crystalline lens (concave mirror). If the person experimented upon be made to look fixedly at objects placed at different distances, the only change in the three reflections which we have mentioned will be found to take place in that furnished by the anterior surface of the crystalline lens (the reflection *b*). We conclude from this, that in the phenomenon of accommodation the anterior surface of the crystalline lens alone undergoes a change; while, by measuring the image in. question, we find (according to the laws of convex mirrors) that, in looking at an object at a distance, the convexity of the crystalline lens is diminished (since we find that the image increases in size); while if, on the other hand, the object is near, the convexity is increased (the image being then reduced in size).



Fig. 117.—Images produced on the surfaces of the ocular media acting as mirrors (Purkinje's images).*

Therefore, accommodation takes place by the modification of the crystalline lens. We shall examine the other means by which the form of this lens may be changed, when we come to the subject of those accessory membranes, especially the choroid and the iris (the ciliary muscle) which are intended to assist and to modify the working of the essential parts of the eye.

D. *Imperfections in the System of Ocular Dioptrics.*—Considered as a physical organ, the eye is far from being perfect: the various imperfections belonging to similar physical organs are found in it, and are known under the name either of *spherical* aberration or *chromatic* aberration.

The essential part of the organ of the eye being a lens, it so happens that this lens, even when most perfect, does not unite exactly at the same point all the rays which, proceeding from the same luminous source, fall upon the edges or upon the centre of the crystalline lens. The focus of the lens is not, therefore, single in its kind, and it is this which gives rise to the *aberration of sphericity.* We shall see that the

* *a*, Upright image reflected by the cornea. *b*, Upright image reflected by the anterior surface of the lens. *c*, Image upsidedown reflected by the posterior surface of the lens.

iris, like the diaphragms of optical instruments, serves in part to remedy this defect.

The *chromatic* aberration results from the unequal refrangibility of the various colored rays of which white light is composed: by means of this, the eye decomposes the ordinary light of the objects which project it, and we see them more or less colored; the eye, in short, is not a *perfect achromatic organ*. Habit renders us, for the most part, insensible to this defect, but various experiments show it plainly. We will mention only one: after looking at the cross-hairs of an astronomical glass, by a red light, we shall find that, in order to see them with another ray of the spectrum (another color), the position of the ocular or eye-piece must be changed; the eye, when so adapted as to see by the red light, not being adapted to see perfectly by the other rays of the spectrum.

Finally, a certain *irregularity* of curve in the surfaces of the media of the eye constitutes what is called *astigmatism* (or *monochromatic aberration*). *Astigmatism* is such a common defect in the refraction of the eye that it may be said to be found, in a varying degree, in most persons; it does not, however, usually affect the sight so much as to be noticed. *Astigmatism* consists in the more or less sensible curve, from one meridian to the other of the surfaces of separation between the media of the eye (especially the curve of the interior surface of the cornea). Let us suppose a cornea in its normal condition divided into two halves, following the line of its vertical axis, the parts maintaining their original position; the surface of the section will represent a curve of a fixed radius; if the cornea be divided, following its transverse axis, the surface of the section will exhibit exactly the same curve (in a normal, non-astigmatic eye); in other words, both sections will conform to a circumference of the same radius. On the other hand, in an eye affected with astigmatism (as nearly all eyes are) the radius of one will be shorter than that of the other; the two curves, in short, are unequal. It is easy to see that this inequality, if sufficiently great, will interfere with the course of the luminous rays as they penetrate the eye; in fact, if we suppose that the radius of one circumference is considerably shorter than that of the other, we shall conclude that the eye is short-sighted in the one sense, while in another it may be much less so, or not at all, or even may be hypermetropic. In order to remedy this defect in the refraction of the eye, it is plainly

sufficient to make the luminous rays pass through a lens cut in such a manner as to restore the equilibrium between the two meridians, so that the rays, after passing through this lens and through the medium of the cornea, follow the same direction as the rays which pass through an ordinary cornea. The surface of the glasses used for this purpose is cylindrical, instead of being spherical, and they are arranged in such a manner that the convergence which they produce on a single plane corresponds exactly with the plane of that meridian according to which the surface of the cornea of the eye is insufficiently convex: in this way, such want of convexity is remedied.

II. *Enveloping membranes of the eye.*

Beginning from the outside, and going towards the centre of the eye, we find that there are three envelopes of the eye, the *white of the eye*, the *choroid*, and the *retina;* the latter being the membrane which is especially endowed with sensibility. We will consider the two first as protecting envelopes, intended to assist, and even to *modify* the functions of the other and essential portions of the eye.

1. *The Sclerotic.* — The sclerotic coat of the eye forms, as it were, its skeleton. This membrane is intended to preserve the form of the ocular globe, and into it the muscles that move the globe are inserted. It has a fibrous texture in man, but cartilaginous and even bony in birds and reptiles. This white of the eye in front undergoes a change; from being white and opaque, it becomes transparent and colorless, constituting the *cornea*, which we have already studied. The cornea is more convex, and belongs to the segment of a sphere whose radius is shorter than that of the white of the eye, or, in other words, of that of the other portions of the eyeball (Fig. 111, p. 491).

2. *The Choroid Tunic or Coat.* — The choroid coat lines the sclerotic throughout, except where it joins the cornea, and enters the anterior chamber of the eye, where, in front of the crystalline lens, it forms a diaphragm called the *iris*. We have, therefore, to study both the *choroid coat, properly so called*, and the *iris*.

A. The *choroid*, properly so called, is essentially a *vascular* membrane; its inner surface is also lined with a layer of *pigment cells*, of a regularly hexagonal shape; it contains, finally, *muscular* elements, especially in front. Three principal functions are, therefore, assigned to this membrane.

1. As a *vascular organ* (having numerous *ciliary* or *choroid arteries*, and groups of veins, forming the *vasa vorticosa*) its purpose is to serve as an organ of calefaction to the nerve membrane beneath it (the retina). We have seen that those organs which contain numerous nerve terminations, particularly the organs of the special senses, usually have an abundance of blood vessels, as we see in the papillæ of the inner aspect of the fingers, the olfactory membrane, the tongue, etc.

2. *The pigment of the inner surface of the choroid* is of great importance to sight; the retina being transparent, the rays of light fall upon the choroid pigment; the effect produced is not yet perfectly understood. It may be that this layer absorbs the more irritating rays, and serves as a reflecting mirror to the others, which affect the terminal organs of the nerve fibres of the retina; we shall find, indeed, that the free surface of the sensory elements of the retina is turned towards the choroid, and that these elements are, undoubtedly, affected only by the rays reflected in this sort of mirror (Ch. Rouget). This pigment layer is not always quite black. There are various shades in different animals; thus, in the ox, it exhibits metallic reflections exactly resembling the surface of a mirror. This pigment layer, which is so dark and opaque in other parts, is, perhaps, like the black covering with which the inner surface of a camera obscura is lined, to prevent the irregular reverberation in all directions of the rays of light, and thus to promote the distinctness of the sight; animals which have no choroid pigment (*albinos*) are scarcely able to endure a strong light (*heliophobia*). The choroid pigment is, certainly, a valuable aid to sight, and the weakening of the sight in old age is partly owing to a loss of color of the inner surface of the choroid.

3. Finally, the *muscular elements* of the choroid (*ciliary muscles*) which are developed principally in its anterior part, and joined to erectile prolongations (*ciliary process*), are chiefly intended to act upon the crystalline lens, and produce the changes of form which we have studied in regard to accommodation; great differences of opinion, however, prevail as to the mechanism by which the muscular action affects the lens (Fig. 118). The *ciliary muscle* is composed of *longitudinal* and *circular fibres*. The former act by drawing forward, from a fixed point at the junction of the sclerotic coat and the cornea (near the canal of Schlemm, *sinus circularis iridis*), the whole choroid membrane, and, consequently, the

vitreous humor and also the crystalline lens; the latter becomes flattened by the resistance offered to it by the aqueous humor, or else becomes more convex at the centre of its anterior surface, whilst the iris opposes a deformation

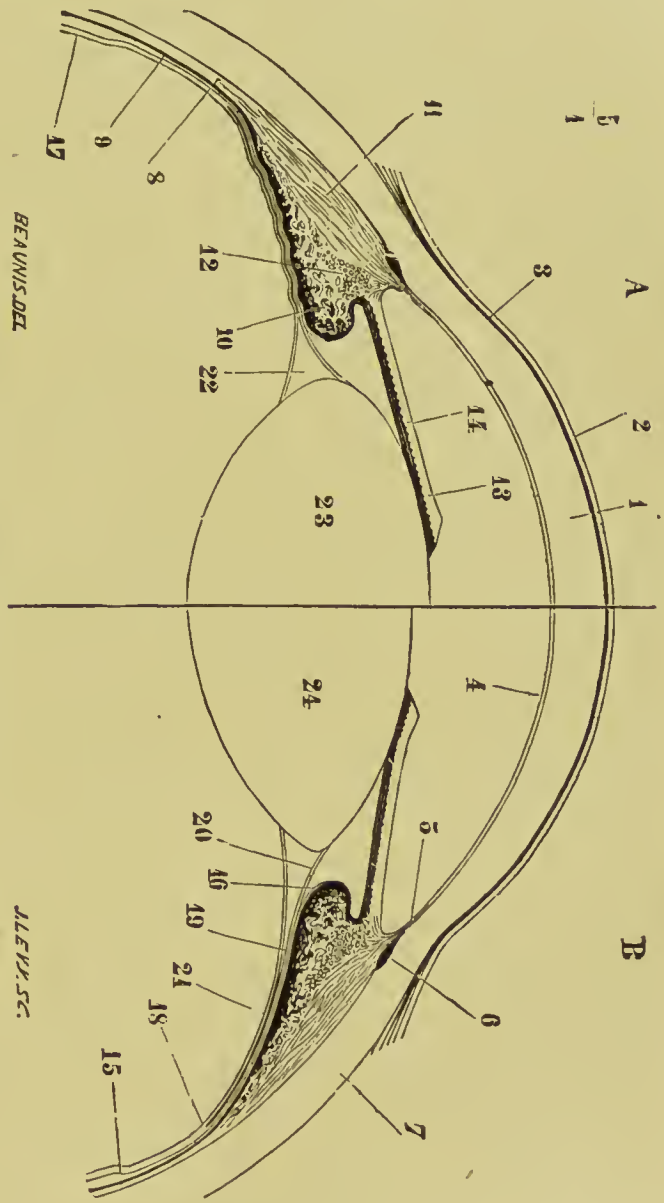


Fig. 118. — Mechanism of accommodation.*

* A, Adapted to the sight of objects near at hand. B, Eye seeing objects at a distance. 1, *Substance proper* of the cornea. 2, Anterior epithelium of the cornea. 4, Demours' membrane (posterior elastic lamina, Bowman). 6, Fontana's duct. 7, Sclerotic coat. 8, Choroid coat. 9, Retina. 10, Ciliary process (or fold). 11, Ciliary muscle. 12, Its orbicular fibres. 13, Iris. 23, Crystalline lens, adapted to the sight of objects near at hand (the convexity of the anterior surface being increased). 24, Lens, when seeing distant objects. 15, *Ora serrata.*

of the peripheral part to which it is attached. It is possible, on the other hand, that the *circular fibres*, in contracting, press, by means of the ciliary process, on the circumference of the crystalline lens, which in this sense gives way; yet, owing to its great elasticity, its thickness at the same time

increases, especially in the central part of its anterior surface, this centre being the only part that is free and susceptible of deformation, because the iris prevents any thing of the kind from taking place in the periphery. The space which was supposed to exist between the iris and the crystalline lens, and which was called the *posterior chamber*, has really no existence, the iris coming in immediate contact with the entire corresponding surface of the crystalline lens (Rouget). The contractions of the iris may, perhaps, also affect the shape of the lens; at all events, the iris appears to lend an important aid to sight, since we see persons who, although they possess to perfection the faculty of accommodation, are yet unable to see clearly, because they have lost the power of contracting the iris, which has been destroyed or injured.

Ch. Rouget has shown, in describing the *internal* or annular *ciliary muscle*, that this muscle, in contracting, compresses the irido-choroid venous trunks, forces all the blood to pass through the ciliary process, and thus gives rise to the erection or rigidity of these organs; without these phenomena the ciliary muscles would have no action on the crystalline lens. None of the theories of accommodation were able, by the help of known facts, to explain the direct influence upon the crystalline lens: this effect is produced by the annular ciliary muscle; the first contractions of this muscle obstruct the flow of blood through the veins, and cause the erection of the ciliary process; and, while in this state, these organs become fitted to transmit to the crystalline lens, in a modified form, the pressure exercised by the ciliary muscle.

We see, in short, that the *contractions of the anterior portions of the choroid* coat (ciliary muscle) *have the effect of producing accommodation.* This adaptation is involuntary and spontaneous, and is the consequence of a reflex phenomenon: it seems as if the retina or the central organs of sight, perceiving the confusion of the image produced, reacted upon the ciliary muscles, thereby causing their contraction. The *ciliary* or *ophthalmic ganglion* was long considered as the *centre* of these reflex phenomena, but they are now supposed rather to belong to the cephalic or cerebral portion of the cord (*Pons Varolii quadrigemina* and *corpora*, see p. 59). The muscular fibres of the choroid tunic are *smooth:* this accounts for a certain slowness in the accomplishment of the process of accommodation.

B. The *iris* is really a diaphragm situated in the *camera obscura* formed by the eyeball: its anterior surface is

in contact with the aqueous humor, and is lined with a prolongation of the *membrane of Descemet* (of the posterior surface of the cornea, see Fig. 118, 13). Its posterior surface, as we have said, is in close contact with the peripheral portion of the anterior convexity of the crystalline lens, proving that the so-called *posterior chamber* has no existence. The periphery is continuous with the choroid tunic, to which this diaphragm forms an appendage; its central opening corresponds with the centre of the crystalline lens, constituting what is called the *pupil* of the eye.

The structure of this membrane is similar to that of the choroid: it contains a large number of *vessels*, *pigment cells*, which also form a thick layer upon its deep or posterior surface (*uvea*), and of *muscular fibres*. The latter is the most important element: it consists of fibres arranged in a circle (sphincter of the pupil), and radiating fibres (*dilatator pupillæ*);[1] these fibres appear to be innervated by two different nerves, the *sphincter* or circular fibres by the *motores*

[1] Ch. Ronget's researches do not confirm the theory of the existence of radiating or dilating fibres of the iris. This physiologist has observed that in the iris of birds there are only muscular fibres, arranged in a circle, and which may produce a contraction of the pupil. He shows that the radiating bundles, which are considered as the dilating muscle of the pupil in the mammalia and in man, really correspond with the veins of the iris when devoid of blood. Therefore the iris is not in an *active state* when dilated, as is the case when contraction of the pupil occurs: the latter movement alone is active. A certain muscular arrangement will suffice to explain all the changes of the pupil, if the repose of the iris be represented by the extreme state of dilatation. There is great difficulty in observing this state of repose of the iris: the pupil is seldom found to be entirely dilated, even after death; this is due to the fact that the direct action of light (as shown by Brown-Séquard), and the final contraction that produces cadaveric rigidity in the muscles of animals after death, may each cause a contraction of the pupil, which may last almost for an indefinite period; however, in the state of general relaxation of the muscular system which follows prolonged inhalation of chloroform, a dilatation of the pupil may be observed. Examination of the iris in young mammiferous animals (cat and rabbit), a few days after birth, before the eyelids are open, or before the organ of sight has been excited by light, will show that the pupil is widely dilated, and that the iris exists in the form of a narrow fillet: this appearance is not owing to any want of development, for the induced current of electricity will immediately produce as decided a contraction of the pupil as may be found in the adult.

oculorum (derivations from the lenticular ganglion and nasal branch of the ophthalmic division of the fifth nerve, ciliary nerves to the number of fifteen), and the *dilatator* or radiating fibres by the *great sympathetic nerve*. The pupil dilates when the light is not strong, or when the object presented is at a distance, and contracts when the contrary is the case. These movements are *slow*, the fibres being *smooth muscular* fibres, like those of the ciliary muscle; the movements of the iris, like those of this muscle, have a reflex character, and belong, no doubt, to the same centre of reflexion (see p. 59). The iris appears, however, to be directly sensitive to the action of light. The will has no power to produce any movement of the iris, but this may be done indirectly by looking into space, as if at an object placed at an infinite distance, and the pupil will then dilate; this simple method has been frequently employed, especially in past times, for the purpose of giving an expression of *ecstasy* to the eyes, this feeling invariably being accompanied with great dilatation of the pupil. Some valuable medicinal agents also possess the property of producing dilatation or contraction: the Calabar bean serves to contract, and belladonna (atropine) to dilate the pupil for a longer or shorter space of time.

The pupil is also dilated in certain diseases of the brain and cord. Its normal movements are more active and frequent in some persons than in others. We have already seen that these contractions have only a subordinate position in the process of accommodation, and we may, therefore, close this part of our subject by saying that the iris is simply a *diaphragm which by a reflex action decides the diameter of its own aperture.*

III. *Sensitive membrane or retina.*

The *retina* is an extremely complicated membrane which closely covers most of the inner aspect of the choroid tunic. It is formed principally by the bifurcations or subdivisions *of filaments of the optic nerve*, to the extremity of which special terminal organs are attached. The optic nerve passes through all the tunics or envelopes of the eye, at a point situated a little within the posterior extremity of the antero-posterior axis of the globe of the eye, and, as it reaches the inner aspect of the choroid tunic (Fig. 119, P.), it expands (*optic papilla* or *optic disk*), and thus forms the internal layer of the retina; subsequently the fibres of this layer bend and turn outwards (Fig. 120), forming thus, by their juxtaposition, the substance

of the membrane of the retina. In the course of their short passage, these fibres exhibit swellings, the signification of which is unknown. Some of these form genuine nerve cells, and terminate by dilating into a peculiar element, which is either small and delicate (*rods*, or larger and more bulky

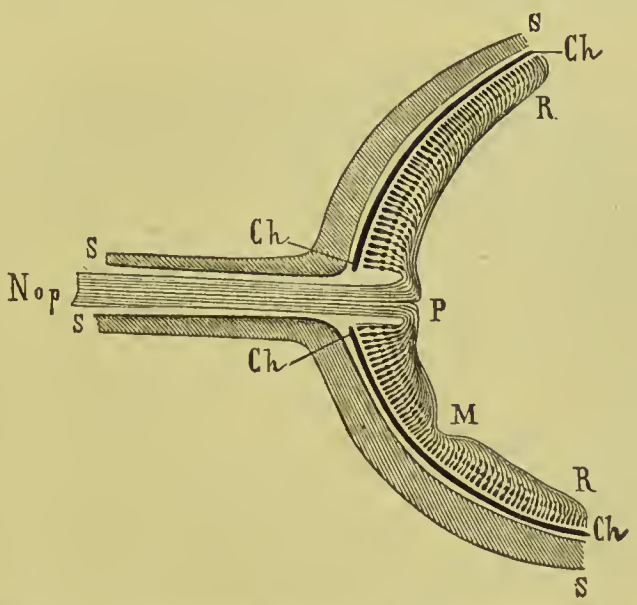


Fig. 119.—Diagram of the retina and the optic nerve.*

(*cones*) Fig. 120); we see, by this arrangement, that the *rods* and *cones* form, by their juxtaposition, the external layer of the retina (Fig. 119); this layer, which is easily separated, was long known under the name of *Jacob's membrane.*

Max Schultze and other German histologists who have lately made investigations on this subject fix the number of layers at ten, which, thus stratified, form the substance of the retina. These are, beginning from within (proceeding from the vitreous humor to the choroid tunic) an internal limiting membrane (Fig. 120, *l*); the layer of filaments of the optic nerve (Fig. 120, *f*); the layer of the nerve cells (*g*); the granular layer (*n*); the internal nuclear division of the granular layer (*k*); the external nuclear division of the granular layer; external granular layer (*k'*); external limiting membrane of Schultze; the layer of cones and rods (Fig. 120, *s*); and, finally, a layer of pigment, which is diffused between the extremities of the cones and rods, and which every thing

* S, S, Sclerotic. *Ch*, Choroid. *Nop*, Optic nerve. P, Its papilla, whence the fibres radiate, and form the retina (R, R). M, Central *fossette* of the retina (or *fovea centralis retinæ*).

tends to prove rather a part of the retina than of the choroid tunic.

The retina is much thinner in one part than in others; in other words, the passage of the nerve filaments from within to without is much shorter; they exhibit no enlargement, and end directly in their terminal organ. This point, which is

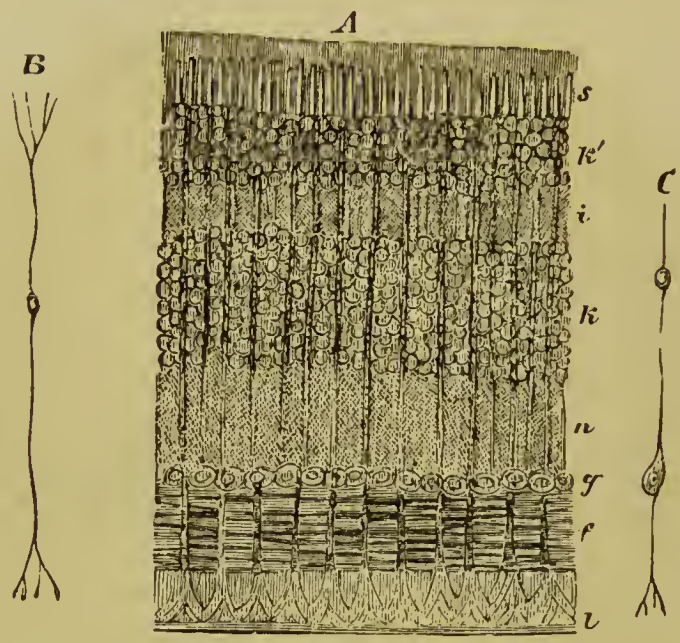


Fig. 120.—Elements and structure of the retina.*

tinged yellow, is known by the name of *yellow spot (macula lutea)*, and is (Fig. 121) situated a little outside of the optic papilla, or precisely at the posterior extremity of the antero-posterior diameter of the globe of the eye. *At this point, the terminal organs are all represented by cones*, while in other parts the rods and cones are intermixed, the former becoming more rare as we examine the anterior part of the retina, that is, the part farthest from the yellow spot. At this part of the retina (region of the *ora serrata;* see p. 437, Fig. 118, 15), all elements of which partake of the nature of nerves gradually disappear, their place being occupied by connective tissue elements, which are also found,

* A, Vertical section of the substance of the retina, hardened by chromic acid. *l*, Membrane, called the membrana limitans, with the ascending supporting fibres (of Müller). *f*, Layer of filaments of the optic nerve. *g*, Layer of the nerve cells. *n*, Gray layer, finally granular, crossed by radiating fibres. *k*, Interior (anterior) granular layer. *i*, Intergranular layer. *k'*, Exterior (posterior) granular layer. *s*, Layer of the rods and cones. B and C, Detached filaments, enlarged.

though in very small quantities, in the other parts of the retina.

Finally, the retina contains vessels, and terminal branches of the central artery of the optic nerve, which emerges in the centre of the papilla, and surrounds the yellow spot with its ramifications (Fig. 121).

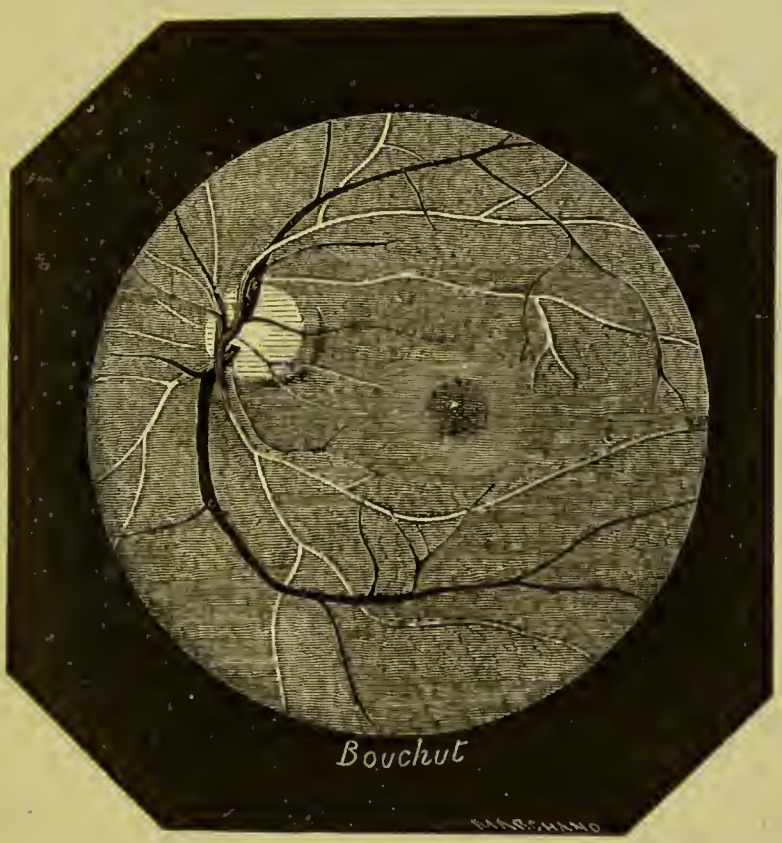


Fig. 121. — Appearance of the posterior half of the retina of the left eye, examined with the ophthalmoscope (Liebreich).

The retina forms essentially the sensitive membrane of the eye; by whatever cause its sensibility is excited, it always gives rise, as a subjective phenomenon, to what is known by the name of *luminous sensation.* If the retina be pricked (Magendie), compressed (*phosphenes, phosphainæ*, studied by Serre of Uzès), twitched by any sudden movement of the eye, or, in short, excited in any way, an impression of light will be produced; the same effect follows the use of electricity. The special method, by means of which the luminous sensation is distinguished from all others, does not, therefore, reside in the qualities which are peculiar to external light; there is no exclusive connection between *light* and *luminous*

sensation. Light is only the usual normal and physiological excitant of this sensation; the retina, being situated in the depth of the eyeball, and protected by the cavity of the orbit, is almost entirely removed from the influence of all other agents than the rays of light; these are able to reach it unobstructed by passing through the transparent media of the eye. We have already seen that in cases where the refringent apparatus of the media of the eye is in working order, the images of external objects are painted (upside-down) upon the retina; an impression is then made upon the membrane, and the excitation transmitted to the cerebral centres (corpora quadrigemina and cerebral lobes), by means of a peculiar mechanism, which we shall endeavor to describe.

The retina is not, however, in every part equally sensitive to light; there is a point which is quite insensitive to it, viz., where the optic nerve (*papilla*) begins, and is called, on that account, the *punctum cœcum.* This may be easily proved by the following experiment: if two small objects, one of which is white and the other red, be placed on the same plane, at a certain distance from each other, and we look at either of them with one eye only, we shall see the other also; but if the latter be moved so as to make its image pass over the whole retina, a moment will come when this image will be formed exactly on the optic papilla; at that moment the object will be quite invisible, being depicted on the *punctum cœcum.* An experiment made by Mariotte consists in marking two black points upon the paper, at a distance of five centimetres from each other, and standing at a distance of fifteen centimetres from the paper, the left eye being closed, while the point on the left side (A) is observed with the right eye; in this position the point on the right side (B) will not be seen, but it will become visible in any other part, whether nearer or farther off. We find, by calculation, that,



in the position indicated, the image of the point on the right side falls upon the *punctum cœcum*, and, consequently, is invisible.

The sensibility of the retina in other parts differs greatly; it reaches its highest point in the *yellow spot* (which corresponds exactly with the *posterior pole* of the eye) and de-

creases in the anterior part; thus it is 150 times less at the equatorial plane of the eye than in the yellow spot or *macula lutea;* thus, if we place two wires very close together, but with sufficient space between them to enable us to distinguish one from the other, and then so direct the eye that their image shall fall, first upon the yellow spot, and then upon the great circle of the eye, we shall find, in the latter case, that the wires to seem distinct must be placed at a distance from each other 150 times greater than when they are painted upon the yellow spot. This experiment is exactly similar to that made in regard to the distance between the points of the dividers, by means of which we estimated the degree of sensibility of the skin (see p. 398).

The yellow spot is, therefore, the principal seat of distinct vision. We make use chiefly of this in order to see clearly, and all the movements of the eyeball are designed to bring the image of the objects observed to this extremely sensitive point in the eye. The entire surface of the retina is about 15 square centimetres, while the surface of the macula lutea is only 1 millimetre; we therefore make use of only $\frac{1}{150}$ part of the surface of the retina for the purpose of distinct vision. Thus, in reading, we see distinctly only two or three words at a time, their image would fall directly on the yellow spot; and the eye must pass over the whole line in order to read it; in other words, it must bring the image of every single word to the sensitive point. In order to decide exactly what is the number of letters, or the extent of surface, painted on the retina, the eyes are fixed, in a dark room, upon the page of a book; the number of letters which can be seen by a flash of lightning or by an electric spark, is then counted, and the dimensions calculated. Starting from this *datum*, the known dimensions of the yellow spot may be calculated.

Having observed the various degrees of sensibility of the different parts of the retina, we must now examine the substance of this membrane, and see whether, among its numerous layers, there is not one which is peculiarly sensitive, and containing an element which is essentially susceptible to the influence of light. A simple experiment will supply us with a sufficiently satisfactory answer to this inquiry: this experiment is known by the name of Purkinjé's *vascular tree*, and consists in the perception of the vessels, or, rather, of the shadow of the vessels of the retina itself. These vessels, which are situated in the anterior layers of the retina, always cast their shadow upon the posterior layers of this membrane,

and we can only suppose that it is the force of habit which prevents our being generally conscious of this shadow; the question was, whether it could not be rendered visible by being thrown, artificially, upon some other part of the eye. This was done in the following manner:[1] the person making the experiment looks at a dark obscurity, while a lighted candle is placed either below, or at the side of his eye (Fig. 122); the rays proceeding from this light (B) will be concentrated by the crystalline lens upon a point very much to one side of the retina, the source of light (the candle) being very far beyond the visual centre. The image of the candle on the retina itself constitutes an interior source of light (B′) which is sufficiently strong to carry a considerable quantity of light into the vitreous body. It is plain that, under the influence of this light, the vessels of the retina (C and D) will cast their shadow upon the posterior layers of the retina, not, however, in the usual portions (that is, C′ and D′). The shadow will be displaced, and thrown upon the side opposite to that of the source of light in the retina, which is on the same side as the candle (the original source of light). The field of vision being then illuminated by a light of a yellowish red, a network of dark-colored vessels is seen to appear, exactly resembling the vessels of the retina, as sketched from an anatomical preparation. (*Vascular tree of Purkinjé.*)

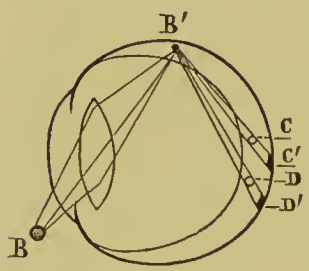


Fig. 122.—Experiment by Purkinjé.*

The *posterior layers* of the retina are, therefore, sensitive to light; but this experiment shows us which of these layers is especially sensitive. By means of a mathematical process which we cannot now describe, and judging by the movements of the shadows of the vessels when the source of light is displaced, or, in other words, by the apparent magnitude of the movement produced in the field of vision by the vascular tree, Helmholtz has inferred that the layer which receives

[1] See Helmholtz, "Optique Physiologique." Traduct. franç. par E. Javal et Th. Klein. Paris, 1867, p. 214.

* B, A candle placed at the side of the eye, that is, as much to the side of the centre of the cornea as possible. B′, *Interior luminous source*, formed by the rays of light concentrated by the crystalline lens upon the extreme lateral portion of the eye. C D, Two vessels of the retina (the size of the retina is here greatly exaggerated). The shadow of these two vessels is seen as if projected at D′ and C′.

these shadows, is separated from these vessels by a distance which is exactly equal to that which by microscopical mensurations of sections of the retina exists between the layer in which the vessels are situated and Jacob's membrane; the *sensitive layer of the retina consists, therefore, of the layer of rods and cones.*

Now that we have seen that the seat of sensibility is in one of the layers of the retina, the extreme posterior layer, we can no longer be content with the empty formula that the *retina is a screen;* nor consider it sufficient to trace the progress of the light through the media of the eye to the surface of the sphere of the retina. The rays of light pass through all the layers of the retina without making any impression, as has been shown, first by Rouget, and since by Desmoulins; on reaching the part where they come in contact with the rods and the choroid tunic, they are reflected; and, as the optical centre obviously coincides with the centre of the retinal curve, the reflexion naturally takes place in the direction of the axis of the rods and cones. The external *segments* of the cones and the rods, however, as has been proved by Schultze,[1] consist of small lamellæ, placed one upon the other; and these, on account of their structure and optical properties, cannot be considered as being susceptible to light, but only as organs which serve to modify the light. It is now generally supposed that at the instant when the light reflected by the *choroid mirror* (Rouget) passes back through the retina, a peculiar transformation takes place in these organs, constituting a sort of necessary intermediation between the physical phenomenon of light, and the physiological phenomenon of nervous excitation. Without exactly defining the intimate nature of the process which here occurs, we may consider it as a *transformation of force;* in other words, the luminous movement (vibrations of the ether) is changed into a nervous movement (nervous vibration. See p. 29). The external parts of the rods and cones are, in themselves, insensitive to luminous impressions, but they form organs of transformation of the waves of light, that is, special agents by which the light is transmitted to the optic nerve.

The internal segments of the rods and cones are then the organs which are essentially susceptible to light. The differences of function, which correspond with the differences

[1] See a *resumé* of these researches. Duval, "Structure et Usage de la Rétine." Paris, 1873. Thèse d'Agrég.

of *form* and *structure* observed between the *rods* and *cones*, from Schultze's researches, appear to consist in this: that the rods are affected only by differences in the *intensity* of the light, while the cones are affected by differences in its *quality*, that is, by its *color*. Thus comparative histology shows that the nocturnal animals (the bat, the hedgehog, and mole), have no cones. We know that it is impossible to distinguish colors in the dark. The night-birds also, have no cones, but simply rods: these are sufficient to enable them to distinguish the differences, not in quality, but in quantity, of the light. On the other hand, the day-birds, especially those which live on small insects of brilliant colors, possess a proportionate and much larger number of cones than man or the other mammalia.

The impressions produced upon the retina exhibit certain interesting peculiarities; one of these being that these impressions *last* for a certain time after the luminous object has ceased to act, and if short luminous impressions succeed each other rapidly, they are at length confused in one continuous impression. Every one knows that a live coal passed rapidly before the eyes produces the effect of a ribbon or circle of fire; because the impression produced, as it passes before one point in the retina, lasts until the end of the next revolution; and these successive impressions are so joined together as to show us, by a line of fire, the path of the luminous point.

On the other hand, a very bright object, placed against a dark background, always seems to us larger than it really is; while a black or dark object, placed against a luminous background, appears smaller. In order to explain this phenomenon it is supposed that the most luminous parts excite, not only those parts of the retina upon which they are depicted, but also the adjacent parts, and thus encroach upon the images of parts less strongly illuminated: this phenomenon is known under the name of *irradiation*. Thus a white triangle, placed against a dark background, appears larger than it really is; while its edges cease to be rectilinear, and appear as curved lines; in short, the surfaces of the sides are convex; a black triangle, against a white background, appears to us smaller than it is, and the surfaces of the sides will be concave. A surface divided into lines of equal breadth, and alternately black and white, will appear to contain more white than black, the white lines seeming broader than the others; this explains why Gothic buildings, blackened by time, and standing out against a brilliant sky, appear to us

lighter and more slender in outline than modern buildings of white stone. M. Le Roux's[1] researches show that the phenomenon of *irradiation* is peculiar to the field of indistinct vision; it increases with the distance from the *yellow spot;* the only radiation which occurs in this part of the retina is that produced by the limits of the acuteness of vision. The radiation in the field of indistinct vision is explained by the progressive interval found between the sensitive elements (rods and cones), as we get farther from the yellow spot where the highest degree of condensation takes place. These *phenomena of irradiation* may, in pathological conditions of the brain, as in delirium, increase to such a degree as to completely upset the reason.

Nearly all the numerous phenomena known by the name of *optical illusions* may be considered either as instances of the *persistence* or else of the *irradiation* of images upon the retina. To these must be added the excitations which take place in the retina itself (*subjective images, entoptic perceptions*). The principal of these are due to modifications in the circulation. We have seen that the retina contains vessels (pp. 443 and 446); these vessels sometimes become congested, and produce compression of the elements of the retina, which, when slight, excites the sensitive membrane, and, when strong, paralyzes it.

Thus, if we lower and raise the head suddenly, we produce *subjective visual sensations*, consisting of bright and dark spots which seem to be impressed on the eye. Many cases of blindness are owing to vascular derangement of the retina, which may be easily discovered in the living subject by the use of the ophthalmoscope.

Looking with the eye into the microscope, especially when there is no object in the field, reveals other entoptic images which are extremely curious; these are *muscæ volitantes* or *specks*, which appear under the form of masses of small and very round globules, all of which have nearly the same size, and are entangled with some sinuous filaments. Ch. Robin has shown that these images are produced by the projection on the retina of the shadow of the globules and the filaments (elements of mucous tissue or embryo connective tissue), which are suspended in the *vitreous body*.[2]

One circumstance which has greatly perplexed physiologists

[1] Académie des Sciences. Avril, 1873.
[2] Ch. Robin, "Traité du Microscope." 1871, p. 437.

consists in the fact that we always see objects upright, and in their natural position, although their image appears upside-down on the retina; this may be, however, readily explained. We see objects erect and not upside-down because our mind carries outwards every impression made upon the retina, and conveys it in the same direction that the rays of light must necessarily follow, according to the laws of optics, in order to produce an impression on any part of the sensitive membrane; in other words, every part of the field of the retina has a part of the external visual field corresponding to it, and these two are so closely connected, that what takes place in one produces the corresponding effect in the other. Thus, when we look at an object so long that the retina becomes fatigued, and the image remains upon it, even when the eyes are closed, the image still appears upright, and not upside down. It is impossible to decide whether this is only the effect of *habit* and of the *education* of the senses, for cases have been known in which persons blind from their birth have seen objects upright and not upside-down, from the very moment that they were able to see.[1]

[1] We have already protested (see p. 447) against the ancient theory that the retina simply resembles a screen. We have seen that it is not enough to trace the passage of a ray of light until it reaches the retina, but that we must examine this after it has entered the sensitive membrane. This examination, made as above (p. 447), gives us exactly what we need for the purpose of explaining why *we see objects upright, although their image on the retina is upside-down.* We know that mechanical pressure of one part of the retina gives rise to a luminous image (*phosphaina*, p. 443), which appears to be situated on the side of the field of vision opposite to that on which the compression is made (see Serre d'Uzès, "Essai sur les Phosphènes ou Anneaux lumineux de la Rétine." Paris, 1853.) "The position of the subjective image of the phosphainæ," says Rouget, "which image is diametrically opposed to the region of the retina excited (although this image is entirely independent of the optical phenomena of vision), proves that the impressions communicated to the extremities of the nerves of the retina by the intermediation of the rods (see p. 447) *are carried beyond the eye in the direction of the prolonged axes of the rods.* The prolonged axes cross each other at the centre of the curve of the retina (in the eye), the rods being arranged according to the rays of this curve. After their intersection, they are outside of the eye, in the part in which the subjective image is produced, the direction being the reverse of that of the rods themselves, the prolonged axes of the rods of the upper region of the retina corresponding to the lower part of the sub-

We must also inquire how it happens that, *having two eyes, we do not see double.* In order to produce a single impression upon the central nervous organs of the brain, any object whose image falls upon both eyes, and, consequently, forms two impressions on the retina, must be depicted upon two *similar points in each retina.* Seeing double, as in *strabismus*, is caused by a want of symmetry between the part disturbed in each retina (see p. 36). We must, however, add that the necessity for the impression being made upon two exactly similar points in the two retinæ, is only the effect of habit, and is by no means *pre-established*, or necessarily connected with the anatomical arrangement of the eye, as implied in J. Müller's *nativistic theory.* This theory has lately yielded to the *empirical theory*, owing to Helmholtz's successful experiments. Preparations made during observation with a compound microscope, in which images are reversed, will enable us to direct the movements of the eye without express attention or care, though these are associated with a perception exactly opposed to our natural habit of vision. Persons who are cross-eyed or who squint (afflicted with strabismus) are not accustomed to blend in one the two images which impinge upon non-coincident points in the two retinæ, and this habit becomes so strong, that immediately after the eye has been restored to its natural position, there is *diplopia* or double vision, though the image of any object be brought to bear upon corresponding or coincident points on the retinæ; the good effects of the operation for strabismus are slowly developed.[1]

jective image (phosphainæ, and those of the lower to the upper part, etc.). This inversion also takes place when, instead of a solid body (the extremity of the finger for the phosphainæ), the reversed image is formed upon the choroid mirror (p. 447), which, after reflexion, causes the rods to vibrate in the direction of their axis. In this manner, the *physical* (optical) *reversion*, produced by the intersection of the luminous rays at the nodal point, is formed and cancelled. In short, *the image, reversed by the optical conditions of the eye, is restored by the physiological mechanism of the sensations when carried to a distance from the point excited*, in the same way as the sensation of tingling of the skin (see p. 56, *Eccentricity of the sensations*), caused by a medullary congestion, extends far beyond the part excited. A better illustration of this is seen in persons who have lost a limb, and feel the sensation in the stump, spread, as it were, to the extremity of the fingers."

[1] See E. Javal, Art. "Diplopie," in the "Nouv. Dict. de Méd. et de Chirur. Prat." Vol. XI. p. 653.

The visual appreciation for perspective is a mental perception. The stereoscope produces a complete illusion of this kind, doing for the mind what the latter would otherwise be obliged to do for itself. In short, according to Helmholtz, in the use of the stereoscope, we are conscious of two simultaneous sensations which are quite distinct from each other; the blending of these two into a single image of the external object is not caused by any *pre-established mechanism* for the excitation of the organ of sense, but by the *exercise of the intellectual* faculty.

A satisfactory answer to questions of this kind is to be found in the case of persons who are born blind, and have been successfully operated upon. When they first receive their sight, their visual *impressions* are the same as ours, but the centre of visual *perceptions* has not received the same education, in regard to its relation with other centres; they lack what we have acquired. They usually imagine, when they behold the outer world for the first time, that every thing which they perceive touches their eyes; they have neither the power of localizing nor of interpreting the impressions made upon the retina.[1]

IV. *Appendages of the eye.*

The appendages of the eye consist of the muscles by which the eyeball is moved, and the lachrymal system which protects the front or exposed surface of this globe.

Muscles of the Eye. — If we consider how small a part of the retina is really sensitive, we shall understand the importance of the movements of the globe of the eye or eyeball. The eye may, indeed, be considered as a somewhat narrow tube, which we can turn in any direction, for the purpose of bringing the image of external objects into its deep median part. These movements are effected by the muscles of the globe of the eye. These muscles are, first, the *recti muscles*, whose action we can readily understand. These are either *elevator* or *depressor* muscles (superior and inferior recti muscles), *abductor* or *adductor* muscles (the external and internal recti muscles). The internal recti muscles are especially important because they serve to make the two visual axes converge towards an object looked at with both eyes. The combination of these muscles gives rise to every possible

[1] See the well-known history of the blind man of Cheselden, in H. Taine, "De l'Intelligence," Vol. II. Ch. 2.

movement. Another group of two muscles exists, whose office it is to produce *in the globe a movement of rotation upon its antero-posterior axis.* These are the two *oblique* muscles. By careful examination of the points of insertion or reflection of these muscles (the pulley (trochlea) of the *trochlearis*, or superior oblique muscle) we find that they both serve to direct the pupil outwards, and also to produce in it a rotary movement, the direction of which, in the right eye, for instance, under the influence of the superior oblique muscle, will be the same as that of the hands of a watch, and the reverse, when under the influence of the small oblique muscle. The purpose of these rotary movements appears to be to counterbalance those of the head, and to maintain the parallelism of the two eyes, when the head is bent on one side or the other.

The oblique muscles also extend from the front to the back, being inserted in the posterior hemisphere of the globe of the eye; they thus draw the globe forwards, and when this movement coincides with that of the recti muscles, which draw the globe slightly backwards, and, especially, with that of the orbicularis palpebrarum, which compresses it from front to back, a sort of compression of the globe of the eye is the result: this compression is intended to prevent too violent congestion of the eye, which is thus compressed as a person would compress a sponge. In the same way, when making violent efforts which send the blood to the head, we instinctively close our eyes, and forcibly contract the muscles attached to them; children who scream so violently that their face becomes suffused with blood, shut their eyes tight while doing so, and, no doubt, at the same time contract the oblique muscles.[1]

[1] See, on this subject, some extremely original ideas of Darwin's on the movements of the face in regard to the expression of painful and sad emotions. "When children scream loudly, the action of screaming produces a great change in the circulation, the blood being carried to the head, and especially to the eyes, producing a disagreeable sensation. Charles Bell has observed that, under these circumstances, the muscles which surround the eyes contract in such a manner as to protect them. This action has become, by the effect of natural selection and inheritance, an instinctive habit. As man advances to mature age, he learns to control, in a great measure, the disposition to cry out, having found indulgence in it painful; he is thus able to avoid the contraction of the corrugator muscles, but can prevent that of the pyramidal

The study of the muscles of the eye is connected with that of the muscles of the eyelids; of these there are two muscles: the *elevator of the upper eyelid* (*levator palpebræ superioris*) and the *orbicularis palpebrarum*. The *levator palpebræ*, which is over the *superior rectus muscle* of the eye, seems almost superfluous, for the last-mentioned muscle, by the fibres which connect it with the upper eyelid, would be sufficient to raise the latter at such times as it directs the pupil upwards. The elevator muscle serves, however, to keep the palpebral aperture wide open, and, during our waking moments, it reposes only for a few seconds at a time, and at irregular variable intervals, when the eyes are closed by winking. The orbicular muscle is, like all other sphincters, formed of fibres in the form of a loop or a circle, but exhibits on every side, and especially on its nasal aspect, genuine insertions in the form of bony adhesions, so that in contracting, the palpebral opening is reduced to a transverse slit, instead of to a point: this is also owing to the fact that the eyelids contain, in their substance, thick layers of resisting fibrous tissue (called *tarsal cartilages*). The functions of this sphincter appear to be supplementary to that of the orbicular muscle of the iris: like the latter it contracts under the influence of sensations on the retina, as, for instance, when the light is too strong; but it also contracts under the influence of reflex irritations originating at the cornea. Thus it is extremely difficult to keep the eye open when any foreign body touches the surface of the cornea, and diseases of this surface frequently give rise to actual spasms of the eyelids.

The Lachrymal Apparatus. — This is composed of a *gland* which secretes the lachrymal fluid or tears, *eyelids*, whose office it is to spread this fluid over the anterior surface of the globe of the eye, and, finally, of a series of *tubes*, by which the fluid is pumped up, and carried into the nasal chambers.

The *lachrymal gland*, which is formed of lobules similar to those of the salivary glands, is situated in the upper part of the outer angle of the eye; gravitation is sufficient to convey the secretion to the external surface of the globe; this

muscles of the nose, which are little affected by the will, and only by the contraction of the internal fibres of the frontal muscle; it is precisely the contraction of the centre of this muscle which raises the inner extremities of the eyebrows, and imparts the characteristic expression of sadness to the face." (Léon Dumont, "Expression des Sentiments, d'après Darwin," in "Revue des Cours Scientifiques." Mai, 1873.

consists of a limpid, colorless, and alkaline fluid, containing a small quantity of albumen and salts, especially chloride of sodium. The *tears* are diffused over the eye, from its outer to its inner angle, by means of the movements of the orbicular muscle alone; the winking of the eyes spreads the tears over the conjunctiva; all the surfaces, in fact, which are moistened with the tears, are covered by a mucous surface, called the *conjunctiva*, which extends from the posterior surface of the eyelids to the anterior surface of the globe of the eye (upper and lower portions of the conjunctiva), and lines the extreme anterior portion of the sclerotic coat, as also the cornea, as we learned while studying that membrane (anterior epithelial coat). The winking of the eyelids thus secures the translucency of the cornea, by the diffusion of a liquid which constantly moistens it, and forms, at the same time, such a delicate and uniform covering that vision is not obscured. *Winking* may therefore be said to be to the eye

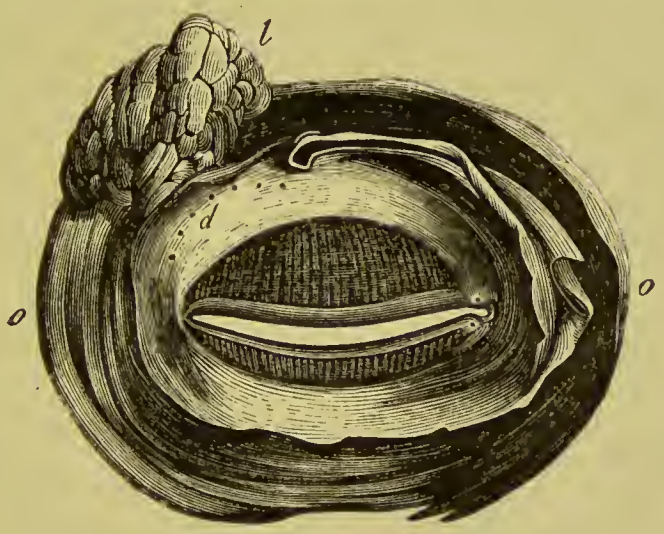


Fig. 124.—Lachrymal apparatus.*

what *deglutition* is to the ear (see p. 222), both movements being intermittent and very frequent. One of the earliest effects produced by paralysis of the eyelids is inflammation of the cornea, which, not being protected by the diffusion of the tears, becomes liable to injury from the air and dust.

* Lachrymal apparatus seen from the conjunctival surface of the eyelids. Meibomian glands are seen to run along the edge of the eyelids. *l*, Lachrymal gland. *d*, Orifices of its seven or eight excretory ducts, at the external angle of the upper conjunctival *cul-de-sac;* at the inner extremity of the edges of the eyelids are seen the orifices of the lachrymal points (in the lachrymal tubercles). *o*, *o*, Orbicular muscle (orbital portion).

The secretion of the tears is constant; it is increased by moral causes, or by reflex irritations of the cornea, but sometimes also from the nasal mucous surface or from the retina. If the cornea be irritated by any foreign body, a hypersecretion of tears follows from the irritating nature of the substance that is dissolved or carried away. This secretion is produced by a reflex phenomenon exactly resembling that which governs the secretion of the saliva. The centrifugal nerve of this reflex action is the *lachrymal nerve* (a branch of the ophthalmic nerve coming from the fifth pair). The hypersecretion of tears which, by a reflex action, follows the irritation of many of the cranial nerves (the frontal, the nasal, the lingual, the glosso-pharyngeal, and the pneumo-gastric nerves), discontinues after section of the lachrymal nerve. According to Demtschenko, irritation of the great sympathetic nerve also causes lachrymal hypersecretion, in the same way as we have seen that it occasions the secretion of saliva (see p. 218); in this case, however, the tears are of a peculiar nature, resembling the saliva under similar circumstances; the secretion is thick and cloudy, while that following irritation of the trifacial, is limpid and transparent[1] (compare with this what is said on p. 219).

The tears evaporate to a certain extent, but a portion always remains; this portion is prevented from flowing over the eyelids and running down the cheeks, by means of the fatty secretion of the *meibomian glands* (see *sebaceous* glands and their functions); these latter are found on the edges of the eyelids, and are more numerous in the inner angle of the eye. From here the tears pass (Fig. 123), by the *puncta lachrymalia*, successively through the *lachrymal canals*, the *lachrymal sack*, and the *nasal duct*, until they reach the nasal chambers, at the anterior portion of the inferior meatus. Many reasons, some of more weight than others, have been suggested, in order to account for the passage of the lachrymal fluid through this series of tubes; some have supposed it to be produced by *capillarity*, but this physical force, by means of which a fluid penetrates a small empty tube, is rather a hinderance than an aid to movement, if the tube is full.[1] This is likewise true of the comparison of the lachry-

[1] Demtschenko, "Zur Innervation der Thränendrüse." Pflüger's Archiv., Sept., 1872.

[1] See Foltz, "Des Voies Lacrymales." "Journal de Physiologie," by Brown-Séquard. Vol. V., 1862.

mal tubes to a *siphon*. It seems most probable that in the movements of inspiration, the rarefaction of the air in the nasal chambers occasions an *aspiration* in the nasal duct, and consequently by attraction through the whole series of tubes and sacs; in the normal state, this slight aspiration is sufficient to give rise to the passage of the tears; thus, when the tears flow in great abundance, we facilitate their passage by short inspirations or *sobs*. The lachrymal tubes are furnished with valves, varying in number, but all so arranged as to allow the tears to flow in one direction only, and to prevent any reflux.

Not only does the passage of the air through the nostrils enable us to understand how the tears flow into the nasal tube, but it appears that, on the other hand, the tears serve to lubricate the respiratory organ, and to counteract the drying effect caused by inhalations of dry air; the entrance to the air-tubes is moistened by means of the vapor which is given off in the air inhaled, and the tears apparently assist in maintaining that state of moisture in the lungs which is so favorable to the *exchange* of the gases (L. Bergeon). The lachrymal system, the product of which always flows into the nostrils, is found even in the ophidia, although their eyeball being hidden behind the tegumentary system, is completely beyond the influence of evaporation. On the other hand, animals, such as the cetaceans, which continually breathe an air saturated with moisture, are the only ones without lachrymal glands.[1]

[1] See A. Estor, "Physiologie Pathologique des Fistules Lacrymales," in "Journ. de l'Anat. et de la Physiol.," by Ch. Robin. Janvier, 1866.

PART TENTH.

URO-GENITAL APPARATUS.—EMBRYOLOGY.

Origin and Development of the Uro-Genital Apparatus.

The *uro-genital* mucous surface and its appendages, on their first appearance, are only a portion of the alimentary canal, of the *mucous layer of the blastoderma*. At the period when the intestinal canal exists only in the form of a tube, its middle portion communicates with the germinal vesicle, and each end terminates in a *cul-de-sac;* on its lower part may be seen a protuberance (B), (Fig. 124), and a partition (E) which separates the primitive tube from the later protuberance; in this protuberance, which becomes more and more prominent, may be found two cavities: 1. The older cavity of the digestive tract or tube, which will later become the rectum; and, 2. In front a *uro-genital* cavity or *sinus uro-genitalis*, from which are formed every part of the urinary and genital organs.

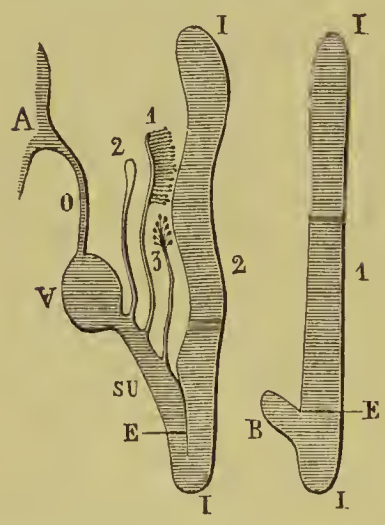


Fig. 124. — Diagram of the formation of the uro-genital organs.*

* 1. I, I, Intestinal tube, with the protuberance B, which will soon be separated by the partition E.

2. The partition has extended; the protuberance B is very much developed, and has given place to the allantoïs A (the commencement of which, the pedicle, can only be seen), and successively, proceeding from the allantoïs towards the intestinal tube, the urachus O, the bladder V, the genito-urinary sinus SU, which has also given off three protuberances: for the Wolffian body 1, for the duct of Müller 2, and for the kidney 3.

In fact this uro-genital sinus (beside the allantoïs, Fig. 124, A, that we shall examine further on) gives origin to three *protuberances* or *cæca* on each side; these elongate in the direction of the superior portion of the germinal vesicle.

1. The first of these protuberances, or, more properly speaking, *germs* (Fig. 124, 1), itself gives rise to lateral vegetations, from which a penniform organ is formed; this is the *Wolffian body*, which in fœtal life is developed to a great size and occupies the largest portion of the abdominal cavity. At this same period it comprises elements analogous to the *glomeruli* or *corpuscles of Malpighi* in the kidney, and seems to possess the same functions that afterwards belong to this latter organ; in consequence of which function the Wolffian body has been called the primordial kidney (Jacobson, Rathke). But, towards the close of the first half of fœtal life in the female fœtus, these organs become atrophied and disappear, whilst, on the other hand, a portion of the male genital organs is developed from them.

2. The second protuberance or cæcum elongates without presenting secondary vegetations; this forms a single tube known by the name of *Müllerian duct* or *organ of Müller* (Fig. 124, 2). This is essentially arranged for the formation of the most important portions of the female genital organs, Fallopian tubes and uterus; in man they form comparatively useless rudimentary vestiges of the embryonic state, such as the *utriculus prostaticus* (*prostatic vesicle*), and a small appendage of the epididymis, the *corpora Morgagnii*, *hydatids of Morgagni*.

3. The third protuberance or cæcum (Fig. 124, 3) presents quite a number of secondary vegetations, originating and radiating from the end of the tube. These secondary protuberances assume the form of canaliculi placed side by side, interlace and finally converge in a little vascular tuft, against which, as it were, their extremity abruptly terminates in a cæcum; beyond this point they are not developed. Each of these embraces, by its cæcal extremity, a vascular tuft; this latter fills up the interior of the hollow of the *cul-de-sac* in such a way as to be lodged in a terminal capsule. Thus are formed the *uriniferous* tubes and the *malpighian corpuscles* (*glomeruli Malpighii*), in one word, the kidney.

Finally, beyond these three protuberances on each side, the anterior extremity of the *uro-genital sinus* is developed, and constitutes the *allantoid* canal (*urachus*) and the *allantoid bladder* (*vesicula allantoidiana*, Fig. 124, 0, A), whose func-

tions we shall presently study when we consider the placenta. We will in this place only mention that the allantoïs and its canal, the urachus, both disappear in the adult. The inferior portion of the canal alone remains, and being developed to an enormous size, constitutes the reservoir, called the *bladder*.

This rapid review of the origin of the genital and urinary organs exhibits a close relationship between these two systems, and consequently teaches the close analogy between their epitheliums; since these mucous surfaces always originate from the epithelium of the *sinus uro-genitalis*, which latter is an offshoot from the *intestinal epithelium*, that is, the internal layer of the blastoderm.

We shall study in succession the *urinary* system and the genital system of the male and the female. We shall elsewhere recur to the embryological conditions of the two latter, which alone furnish facts that establish the homology of the organs of the two sexes.

I. URINARY APPARATUS.

A. *Secretion of urine.*

In their structure the *canals* or *tubes* which compose the renal parenchyma resemble the sudoriferous glands. These are straight tubules in the medullary portion of the kidney (ducts of Bellini, Fig. 125), then becoming convoluted or twisted together (ducts of Ferrein) in the *cortical* substance.[1]

[1] The connections of the straight tubules, of the convoluted tubules (*tubuli contorti*), and of the glomeruli (*Malpighian corpuscles*) of the kidney, especially demonstrated by Schumlansky, Bowman, and Isaacs, have met with formidable antagonism from Müller and Henle. Henle especially has undertaken to describe some looped tubules among the uriniferous tubes, which he considered as terminating in *culs-de-sac*, or dividing into smaller tubuli. There are, indeed, very remarkable looped tubules in the kidney, but a study of these tubules, called tubules of Henle, undertaken by Kölliker, Zawarickin, and especially Schweigger-Seidel, has demonstrated that these formed no separate system, as was formerly supposed by Henle (see "Traité d'Anatomie," by Cruveillier and M. Sée. 4th edition, 1869). By the action of acids on the substance of the kidney, Schweigger-Seidel was the first to show that Henle's tubules have the most intimate connection with the classical straight and convoluted tubules of the kidney, and that they are not in the least degree blood-vessels, as Chrzon-

At this point each of these terminates in a sac-like dilatation into which projects, *hernia-like*, a vascular tuft (*glomerulus Malpighii*), formed by the capillarization of an arteriole

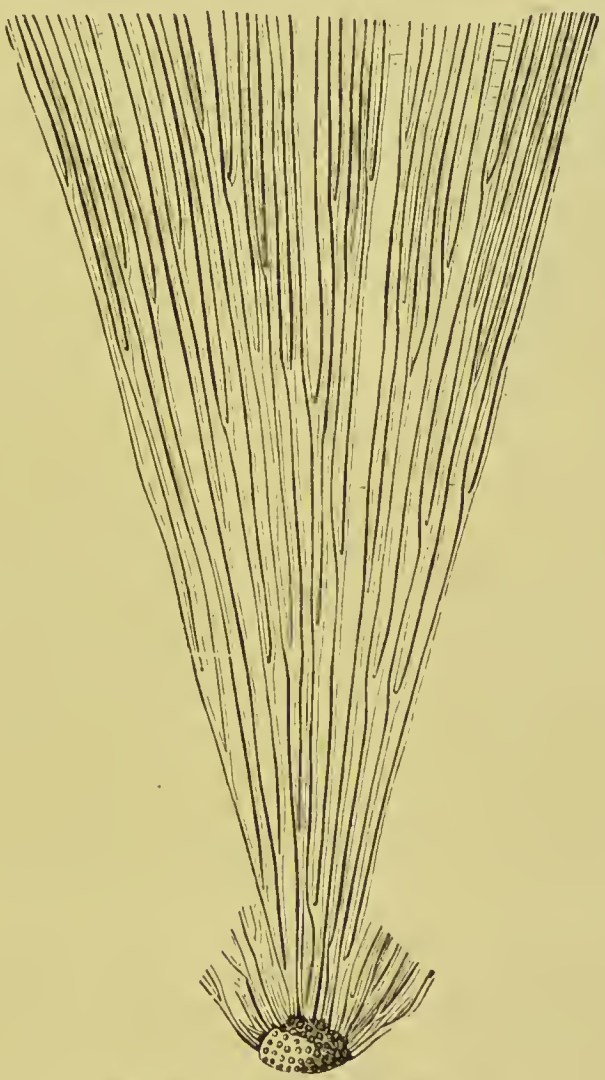


Fig. 125. — Tubuli of the kidney.*

(*afferent vessel*), Fig. 125, a. These capillary tufts converge to form a small *efferent vessel* which leaves the glomerulus at

sczewsky and Sucquet tried to prove. These looped tubules (going from the glomeruli towards the medullary substance of the kidney, and, in fact, following the same course as the urine) are continuations of the tubes of Ferrein, whose walls at a certain place become much smaller, rectilinear, and descend in the medullary substance

* Origin and dichotomy of the uriniferous canaliculi in the medullary substance of the human kidney (tubes of Bellini). (Schumlansky.)

the same or near the point where the afferent vessel enters (Fig. 126, *p* V). But it must be noted that the efferent vessel does not immediately reunite with its fellows to form the renal vein; almost immediately after it has left the glomerulus it divides again and forms a capillary system in the renal parenchyma (RC), the vascular network of which interlaces with the uriniferous tubes. This efferent vessel does not merit the name of a vein; it belongs to a separate system which we might perhaps consider as a *renal portal vein*, since it is intermediate between two capillary systems, viz., the glomeruli and the renal parenchyma; the true origin of the renal vein is subsequent to these last-named capillaries.

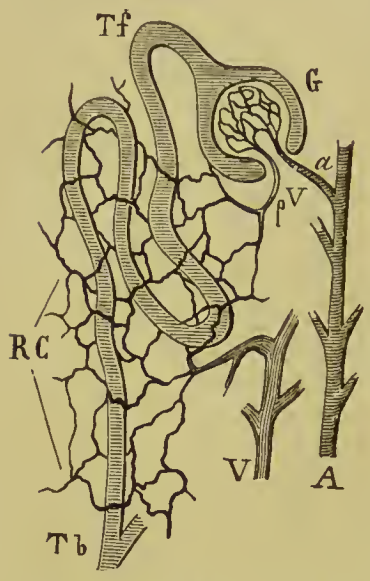


Fig. 126. — Diagram of the kidney and its circulation.*

This arrangement of the vascular system in the kidney forms the basis of all the modern theories upon the *urinary secretion;* a *filtration* is the fundamental process on which these theories depend.

If we recall the fact that differences of pressure between the various parts of the circulatory system do not bear any relation to the especial form of these parts (trunks, small vessels, or capillaries), but to their distance from two extreme points (left ventricle and right auricle) of the origin and ter-

of the pyramids of Ferrein (alongside of the tubules of Bellini), then reascend again, becoming larger, and go into the cortical substance; there these tubes take a new direction, and finally continue with the true tubes of Bellini. In brief, the tubes of Henle become loops in form of inverted siphons between the tube of Ferrein and that of Bellini. The only physiological knowledge that we at present possess of these looped tubes is dependent on their constriction in the descending branches, and the dilatation in their ascending branches. Yet their epithelium is clear and transparent in the straight and descending branch, turbid and granular in the large and descending portion (towards the bases of the pyramids). (See Ch. Fr. Gross, "Essai sur la Structure Microscopique du Rein." Thèse de Strasbourg, 1868, No. 95.)

* T*b*, Straight tube of Bellini. T*f*, Convoluted tube of Ferrein. G, Glomerulus, with its vascular tuft. *a*, Afferent arteriole, going to the capillaries of the corpuscle. *p*V, Efferent vessel forming smaller capillaries among the renal tubuli in RC, before forming the true venous vessel V.

mination of the vascular apparatus, we can then readily understand that, in the two systems of renal capillaries, the pressure will not vary from that of the ordinary capillary system (of the limbs, for instance). Whilst (Fig. 127) in these last, on account of their intermediate position (see *Circulation*, p. 151) between the origin of the arterial cone and the termination of the venous cone, the pressure is also intermediate between the two corresponding extreme pressures; that is, this pressure may be represented by $\frac{12}{100}$ (that at the origin of the aorta $= \frac{25}{100}$, and that of the termination of the vena cava $= 0$ or $\frac{1}{100}$); this is not so in the renal system; for this number $\frac{12}{100}$ represents, not the pressure of either of the two kinds of capillaries, but the pressure of the efferent trunk of the glomerulus (of the vessel *p* V in Fig. 126); because, as shown by the diagram (Fig. 127, 2) it is this efferent trunk (S P) which is placed midway between the distance of the left ventricle (V) and the right auricle (O).

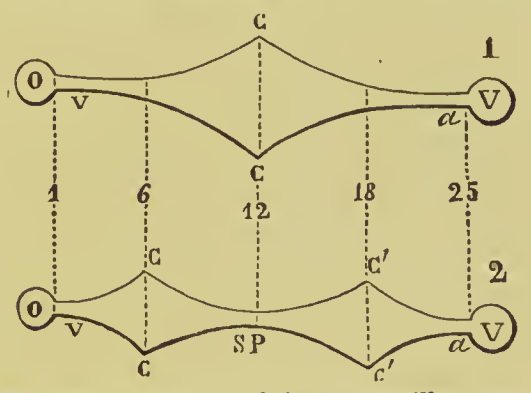


Fig. 127. — Diagram of the two capillary systems in the kidney or the renal portal vein.*

As for the pressure in the renal capillaries, a similar calculation will show that in the glomerulus, that is, in those capillaries which are placed between the arterial system properly so called and the efferent vessel (S P, Fig. 127), the pressure should be intermediate between $\frac{25}{100}$ and $\frac{12}{100}$, viz., $\frac{18}{100}$. In those capillaries which follow the efferent vessels which wind about the uriniferous tubes to give origin to the vein properly so called (Fig. 126, RC) and (Fig. 127, C′C′), the pressure should be intermediate between $\frac{12}{100}$ and $\frac{1}{100}$, or equal to $\frac{6}{100}$ (see *Circulation*, p. 151).

* The superposition of the numerals show that the pressures are not the same in the capillary system of the general circulation and in each of the capillary systems of the kidneys (at the glomerulus, and in the interstices of the tubes).

1. General circulation. V, Ventricle. O, Auricle. *a*, Artery. V, Veins. C C, Capillaries (pressure, 12).

2. Renal circulation. V, Ventricle. O, Auricle. *a*, Renal artery and afferent vessel of the glomerulus. *c′*, *c′*, Capillaries of the glomerulus (pressure, 18). SP, Efferent vessels of the glomerulus (representing the trunk of a portal vein, the vessel *p*V of Fig. 126). *c*, *c*, Capillaries resulting from the dichotomy of this efferent trunk amongst the renal tubes (pressure, 6). *v*, Renal vein, correctly called, following this second system of capillaries.

In a general way, then, it may be said that the *blood of the capillaries in the glomerulus is subjected to quite a considerable pressure, and that in the interstitial or parenchymatous capillaries there exists a pressure less* than that of the blood in the ordinary capillaries.

The intensity of the pressure in the first system has attracted the attention of every physiologist, and all admit that in this system there should occur a mechanical filtration which would be the first phase of the source of the urinary secretion, but there is a want of agreement with regard to the character of the liquid filtered. Some (Bowman) consider that it is simply water; others (Ludwig) that it is urine, but largely diluted, which by the loss of a portion of its water will become the urine that is afterwards poured into the bladder.[1]

If we apply here the information that physiology of the capillaries of other portions of the body has supplied, and recollect that the capillaries of the glomerulus present a structure similar to those of every other region; we ought to conclude that in these capillaries there is normally produced, in view of the normal and permanent excess of the pressure, what is abnormally produced in every other region when the blood pressure is exaggerated. Following out this suggestion, when a ligature compresses the veins of the forearm, when from a pathological cause the abdominal venous circulation is arrested; in brief, at any time that the pressure in the capillaries is increased, these latter will allow the liquid portion of the blood to filter out through their walls, with all the constituent elements of the serum, viz., water, albumen, etc. The supposition is, then, authorized that the same phenomenon will occur in the glomerulus, and that this latter does not allow pure water, but the serum of the blood without making any distinction between its elements, to pass into the uriniferous tube.

This view is fully confirmed by an experiment already performed in nature by pathology: when an uriniferous tube, in any part of its course, becomes obliterated, its initial portion continues to receive the products of filtration in the glomerulus which have accumulated in the obliterated portion; this latter enlarges, and finally forms a cyst of variable size. Now if the contents of similar cysts be analyzed, these are

[1] See Cl. Bernard, "Leçons sur les Liquides de l'Organisme." Vol. II. Leçon 6.

found to consist of a liquid identical with the serum of the blood: *this proves that the serum filters out in the glomeruli.*

This is the first phenomenon of the secretion of urine: *filtration of the serum of the blood.*

We will now learn how the product of filtration in the glomeruli is transformed into urine: this transformation evidently occurs in the sinuous course of the uriniferous tubes (*tubuli uriniferi*), through which the filtered liquid is carried from its original point to the *pelvis* of the kidney.

Those authors who see in the filtered liquid simply pure water cannot conceive the formation of urine except by a *secretion* from the walls of the uriniferous canaliculi, a secretion to which is *added* the substances that the urine should contain. On the other hand, those who, like Wittich and ourselves,[1] see in the filtered product a very diluted urine, believe that the formation of the urine is accomplished by a simple aqueous reabsorption, effected by the medium of the uriniferous tubes, thus giving to the urine the desired concentration.

As we have demonstrated that the product of the filtration in the glomeruli is the serum of the blood; and as a comparative study of the composition of both serum and urine shows, in a general manner, *that in the composition of the two liquids the serum differs from the urine only by the presence of albumen;* we are induced to believe *that the formation of urine consists in the absorption of this albumen*, an absorption that necessarily occurs along the circuit of the uriniferous tubes.

This explanation of the *second phase* of the *work of the kidneys* is a necessary consequence of the theory advanced in the earlier portion of this book; it is true that there is no way by which we can verify the theory; but we may be allowed to examine whether what we know of the structure of the kidneys is favorable to this view.

In the first place, the length and the form of the convoluted tubes, a form so closely resembling the intestinal convolutions, naturally leads to the theory that we have also in the kidneys a system or apparatus for absorption, and in which the course of the liquid is retarded for the purpose of favor-

[1] V. Wittich, Virchow's "Archiv für Pathologische Anatomie." Vol. X. — Donders, "Physiologie des Menschen." Leipzig, 1859, Vol. I.

ing a prolonged contact with the walls of the tubes. In the second place, the lining epithelium throughout the principal part of these tubes is clear and transparent, unlike the granular epithelium of the secreting glandular sacs;[1] and moreover, whilst this latter reveals its function by the numerous cellular detritus that are found in the secreted liquid (since in a general way it may be stated that every secretion of this kind is the result of a desquamated epithelial moulting); on the contrary, the epithelium of the uriniferous tubes shows little if any of this detritus, the urine being a liquid which is very poor in globular elements. This epithelium thus appears destined to preside over an absorption, and undoubtedly does so in an active manner, by removing from the serum an element so essential to the organism, and of which the blood cannot be deprived without risk, viz. albumen. Should this epithelium become diseased, it will no longer fulfil its function, and albumen will not be absorbed, but will appear in the urine; this latter accident occurs in Bright's disease, which is precisely a disease of the kidney epithelium. Those writers who would allow for this epithelium a function of secretion, by means of which the wall of the tube would add to the filtered water the constituent elements of urine, find themselves in face of a singular contradiction when they desire to explain the pathogeny of albuminuria; because, as a necessary result of their theory, when this epithelium is diseased, it must secrete, not only the solid matters which normally belong to the constitution of urine, but in addition to these a new element, albumen: thus we should have, as the sole example in the organism, this epithelium performing its function with more activity in a diseased than in a normal state; producing all the elements belonging to its normal condition, and others besides.[2]

We know already that a feeble pressure in the blood-vessels conduces to a favorable absorption (see p. 273). We have also seen that in the capillaries which are near the uriniferous tubes the pressure is less than in the ordinary capillaries. The interstitial network of blood-vessels is then

[1] See the note on p. 533.

[2] These considerations of pathology, which belong to the theory of urinary secretion, as we have just evolved, have been lately developed, especially in relation to albuminuria, in a thesis by G. Fayet: "Essai sur la Pathogénie de l'Albuminurie." Montpellier, 1872. See, also, J. B. Olinger, "Esquisse de la Physiologie de la Fonction Urinaire." Paris, 1873, No. 84.

admirably arranged to receive the albumen reabsorbed by the epithelium; and so, too, are the capillaries of the malpighian tufts (the glomeruli) arranged to allow a filtration of the serum; in fact, it is owing to this circulatory system, which we have called the renal portal vein, that the solution of this twofold phenomenon may be found, viz. filtration and reabsorption, which constitute the two phases essential to the secretion of urine. Comparative physiology illustrates this twofold phenomenon still more perfectly: among the ophidians (snakes, etc.), which secrete a solid urine, a liquid is found at the beginning of the uriniferous tubes, which gradually becomes thickened in its course, until it finally acquires the characteristic semi-solid consistency.

Thus, to sum up, the secretion of urine is composed of two distinct phases: 1, *A phenomenon of simple filtration in the glomerulus;* 2, To this purely mechanical phenomenon there succeeds a *vital work on the part of the globular elements of the epithelium of the uriniferous tubes.*

This epithelium of the uriniferous tubes, then, simply absorbs, but does not secrete; formerly it was supposed to have something to do with the formation of urea, but it is now proved that all the urea found in the urine is primarily contained in the blood. The origin of urea in the kidney is reduced to a simple question of experiments, the results of which show that urea pre-exists in the blood, and is not formed in the kidney; that the blood of the renal vein normally contains less urea than that in the renal artery; that ligation of the ureters produces the sume symptoms as ablation of the kidneys. In France, Prévost and Dumas, Ségalas and Vauquelin,[1] Cl. Bernard and Barreswil, Picard[2] (Thèse de Strasbourg, 1856), have arrived at these results; yet, in Germany, their researches have been opposed on account of an assumed error in the estimation of urea; Oppler, Perls, Hermann, Hoppe-Seyler, and Zalesky contend that a large amount of urea is formed in the renal tissue, just as ptyaline is formed in the salivary glands; a maceration of kidney gives origin to urea in the same way that a maceration of the parotid gland gives rise to animal diastase. Finally, Zalesky pretends that ablation of the kidneys (nephrotomy) and ligation of the ureter produce different symptoms; that, after

[1] Journal de Magendie. Vol. II. p. 354.

[2] J. Picard, "De la Présence de l'Urine dans le Sang et de sa Diffusion dans l'Organisme."

ligature of the ureter, urea is found in much greater abundance in the blood, and more rapidly induces uræmic poisoning. This question has been decided by the employment of an incontestable means of estimating the amount of urea, viz. by the process employed by Gréhant: with Millon's reagent, or the nitrous-nitrate of mercury, the urea is decomposed into equal volumes of carbonic acid and nitrogen; the especial precision and characteristic feature of this process depends upon the collection of all the carbonic acid and all the nitrogen, that is produced by this reaction, in such a manner that in each analysis the equality of the determined volumes of carbonic acid and nitrogen will render certain that only urea has been decomposed. In this way it has been demonstrated, that the accumulation of urea, after the operation of nephrotomy, occurs in a continuous manner; and that in this case, as after ligation of the ureters, the quantity of urea which accumulates in the blood is equal to the amount that the kidneys would excrete; that after ligation of the ureters, the blood which leaves the kidney contains exactly the same amount as that which enters this organ; that in the normal condition of the blood the renal vein contains less urea than the renal artery, and that this deficit precisely corresponds with the quantity of urea which is thrown off by the urine[1] during the same period of time. We have then the right to conclude in an incontestable manner, that the kidney is simply a filter, in which urea is eliminated, that is, the renal filter can be impregnated with this substance and give it up by drainage.

B. *Composition of urine.*

Urine is secreted during 24 hours in variable quantity, in the normal condition to the amount of 500 to 1500 grammes. This urine is an aqueous solution of various principles: its elements in solution are pretty constant in quantity, the variation being due to the proportion of water; in fact, the urine is more or less *abundant* during health, because it may be more or less *diluted.*

The *quantity of water* in the urine depends upon the conditions of the circulation and blood; as the urinary secretion is a filtration resulting from pressure, when the arterial

[1] See Gréhant, "Cours de l'Ecole Pratique de la Faculté de Médecine de Paris." ("Revue des Cours Scientifiques." Nov., 1871.)

tension increases, more urine, or, correctly speaking, more water will be excreted; so also when the arterial tension is diminished, the urine will be less abundant. Physicians know full well that there is no necessity for prescribing diuretic medicines for patients whose pulse is very soft and feeble, and that in such cases the best diuretic will be a drug that will stimulate the force of the heart and the circulation. With this understanding the urinary secretion is very important, for it forms a sort of safety-valve by means of which the blood is freed of an excess of water. After a meal there is a sort of general plethora, an augmentation of the blood tension, and consequently an abundant and diluted urine will flow (*urina potûs et cibi*). In the morning, however, the urine secreted during a previous night of repose is more concentrated and scanty, because there has been no cause to increase the quantity of liquid in the blood nor its pressure. The lungs eliminate a slight amount of water. A proportion between the weight of the organism and the quantity of solid residue contained in the daily urine may be calculated. Each kilogramme of the weight of the animal is represented by one gramme of anhydrous urine. Yet this proportion may vary according to the season or character of food.

A man weighing 65 kilos. will excrete, on an average, 65 grms. of anhydrous urine. Nearly one-half (30 grms.) of the anhydrous daily urine is represented by a substance, urea, that we have mentioned before when speaking of all of the other liquids of the organism. This substance is a nitrogenous principle. More nitrogen is eliminated in urea than in any other excrementitial product. It has been demonstrated that the urea excreted is almost all (according to Lehmann, four-fifths) that which can be produced from the food we eat; the remaining one-fifth may be accounted for when we recollect that the respiratory excretion, as well as the epidermal exfoliation and the secretion of sweat, contain a small amount of urea. There is also found in the urea about one-fifth of the carbon, which must be added to the 500 grms., that we daily excrete by means of the lungs.

The amount of urea may vary under the influence of certain well-defined conditions; since it is the residue from the combustion of albuminoids in the organism, its abundance will depend upon the amount of animal food contained in nutriment.

In a general way it may be stated that there is a direct

ratio between the degree of animal heat and the amount of urea eliminated (Hepp and Hirtz).[1]

The remaining 35 grms. of anhydrous urine (half the amount eliminated in a day) is distributed as follows:—

There are 15 grms. of matters called extractive, that is, products of incomplete combustion of the albuminoids: to this class belong *creatine*, *creatinine*, etc., but the most interesting of this class is *uric acid*, not found in large quantity, it is true; but which, under certain circumstances, can be accumulated to a large extent, or be retained in the tissues (uric acid diasthesis; gout; *tophus* of urate of soda). In the normal state this substance exists in proportion to the urea, as 1 is to 30; that is to say, that 1 grm. is found in the urine of 24 hours. Its especial characteristic consists in its sparing solubility in water, which dissolves only $\frac{1}{2000}$ of its weight. On account of its difficult solubility we cannot explain how uric acid exists in solution in the urine; it may be in combination with soda as urate of soda; yet, as this latter is scarcely any more soluble than uric acid ($\frac{1}{1500}$), we must suppose that uric acid or the urates are dissolved by the aid of the acid phosphate of soda (that which gives to urine its acid reaction), or by that of the coloring matter. It is known that if urine be allowed to stand while exposed to the air, a species of lactic acid fermentation ensues, by which a large portion of the coloring matter seems to be destroyed and uric acid to be formed. Among many of the herbivora an analogous acid, *hippuric acid*, apparently replaces the uric acid; this former acid is composed of benzoic and glycocholic acid: in fact, man can make this acid appear in his urine by the ingestion of benzoic acid; glycochol or sugar of gelatine is by this means provided by the metamorphosis of the connective tissue.

There now remain but 20 grms. of anhydrous urine for whose composition we must account; these 20 grammes are represented by the salts, of which chloride of sodium forms 8 parts, and various other salts 12 parts (sulphates, phosphates, lactates, &c.). The base of these salts is mostly soda; there are also some salts of lime held in solution by means of an excess of acid. Alkaline urine, as from the herbivora, for instance, is turbid; and horse-urine is employed as a type

[1] See Art. "Fièvre," in Vol. XVI. of the "Nouveau Dict. de Médecine et de Chirurgie Pratiques."

for the designation of urine which is turbid or alkaline owing to some pathological cause, hence called *jumentous urine.* The phosphates are usually made up of the alkaline earthy salts, there being in the urine passed during 24 hours about one or two grms. of phosphate of lime and magnesia. It is worthy of note that the kind of alimentation has a certain influence upon the presence of the phosphates and sulphates in the urine; we usually take but a small quantity of sulphur and phosphorus as contained in the organic products (albumen, proteine, gluten, etc.). When the proteine substances are burnt up in the organism and transformed into urea, they cause an oxidation of the sulphur and phosphorus, and form sulphuric and phosphoric acid. This explains the fact that the phosphates and sulphates simultaneously vary in quantity in the urine, according to the same laws as urea. We have already learned that a certain amount of sulphur (nearly 4 grms. in 24 hours) is found in the bile as tauro-cholic acid.

The pretended Kiesteïne (more properly Kyesteïne), noticed by Nauche and Golding-Bird, occurring in the form of a peculiar albuminoid pellicle floating on the urine of a pregnant woman does not constitute a definite compound. This is composed of an ammoniaco-magnesia phosphate and of a substance not yet precisely determined, called *gravidine* (a particular albuminoid compound) by J. Starck, a caseine substance (the elements of the commencing secretion of milk which passes by reabsorption into the blood and thence into the urine) by G. Bird, mucus and a proteine substance by Lehmann, infusoria and vibriones by Béchamp, etc.

There is nothing precisely known of the influence of the nervous system upon the urinary secretion. From what precedes it is probable that this influence is reduced to a vasomotor action, which modifies the afflux and presence of the blood in the capillaries of the glomeruli and renal tissue.

M. Peyrani has sought, by means of numerous researches on animals, to explain the *part played by the great sympathetic on the urinary secretion.* He determined the amount of urine and urea first secreted during the six hours preceding experimentation, then the six hours during the galvanic irritation of the sympathetic, and again during the six hours succeeding the section of the sympathetic; and observed that this quantity was greatest in those cases where the sympathetic had been cut (a section of the cervical portion of the sympathetic was made), while galvanization of the distal end of the divided sympathetic brought the quantity

of urine and urea much below the standard of health. Vulpian determined more precisely the modification of the urinary secretion by the sympathetic branches; his experiments were made on the *splanchnic nerves*. As soon as either of the splanchnic nerves was cut, the corresponding kidney was injected, reddened, and increased in size; the vein distended, and the blood assumed an arterial brightness; finally, the urine secreted contained a much greater amount of albumen.[1]

C. *Excretion of urine.*

The pressure which causes a filtration of urine pushes it along through the uriniferous tubes, and produces a sort of *vis a tergo*, which sends the liquid as far as the summit of the *pyramids* (*papillæ renales*, papillæ of the kidney), whence it flows out of numerous little pits, the *papillary orifices*, into the calyces of the pelvis; this same force, *vis a tergo*, is continually exerted through the course of the ureters as far as the bladder, for it is hardly probable that the contraction of their muscular walls is called in play to assist by a series of waves the propulsion of the urine; in fact, in cases of extroversion of the bladder in which the ureters open in front of the lower portion of the abdomen, as it were, in open sight, the urine may be seen flowing drop by drop through these orifices only as it is produced, and in no wise is propelled by jerks as would be the consequence of muscular contractions. The ureters open into the bladder by traversing in an oblique direction the walls of this reservoir; when the bladder is very much distended the pressure on these orifices must be quite considerable, and the delivery of a fresh amount of liquid be greatly impeded. At such times the contractility of the ureters will assist by propelling the urine with a peristaltic movement, which will afford sufficient force to overcome the resistance to the passage of urine along the vesical walls.

The *bladder* is a reservoir resulting from the dilatation of the *urachus* or *allantoid pedicle* of the fœtus. Its interior is lined by an epithelium, outside of which are more or less regular muscular layers.

The *vesical epithelium* is of the pavement or stratified form, but its superficial cellular elements are remarkable for their irregularity and oddity of shape (Fig. 128). From the

[1] Vulpian, "Société de Biologie." Mai, 1873.

physiological point of view this epithelium is remarkable for its impermeability; it absolutely opposes the transmission of liquids. A solution of belladonna may be kept in a perfectly healthy bladder for a long time, without risk of poisoning from atropine; so, also, may solutions of opium, without danger of opium poisoning. But if the epithelium is diseased, absorption immediately occurs; and, as an example, when dilute alcohol is injected into the bladder in which there exists catarrhal inflammation, symptoms of alcoholic intoxication are manifested. The vesical epithelium even for some hours after death preserves its vitality and consequently its impermeability. If ferro-cyanide of potassium be injected through a tube, thus preventing contact with the urethral mucous surface, into the bladder of an animal which has just been killed, then the bladder be exposed and a ferric salt placed upon the outside of its walls, no Prussian blue will be seen. This experiment shows that the two salts, which in contact would produce Prussian blue, are separated by an impassable barrier, viz., the epithelium. Yet if by means of a wire the epithelial coat on the inside of the bladder be scratched or destroyed at this point, Prussian blue will be immediately formed. This opposition, then, to the passage of liquids results solely from the presence of the epithelium.[1]

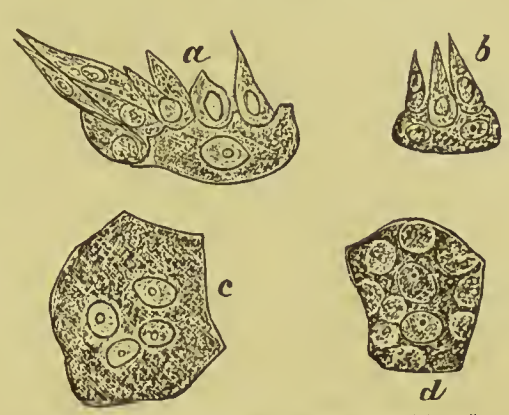


Fig. 128. — Epithelium of the bladder.*

The muscular fibres of the bladder are smooth, and

[1] For a further verification and elucidation of the above statement the reader is referred to Ch. Robin, "Leçons sur les Humeurs." 1867, p. 22. Also, see J. J. C. Susini, "De l'Imperméabilité de l'Epithelium Vésical." Thèse de Strasbourg, 1867, No. 30. The epithelium of the urethra being much less resisting, and possessing a different character (columnar and pavement cells), permits absorption. (See Alling, Thèse de Paris, 1871.)

* *a*, Voluminous cell, with the edges notched; smaller spindle-shaped cells are attached to these edges. *b*, Analogous cells; the most voluminous has two nuclei. *c*, A still larger cell, irregularly quadrilateral, with four nuclei. *d*, Analogous cell, as seen in front, with two nuclei, and pitted, the pits corresponding to the notches of the edges, above. (Virchow, "Path. Cell.," and "Archiv. für Pathol. Anat." Vol. III., Tab. 1, Fig. 8.)

consequently have slow and lazy contractions; but they are, moreover, very elastic, and allow the bladder to dilate readily, as well as the urine to accumulate in large quantity. When this dilatation is pushed to its extreme extent, it becomes a cause of irritation to the muscular fibre, which will then contract, and the bladder expel its contents. We shall soon see that this reaction occasions a desire to urinate. When there is inflammation of the bladder, its muscular walls are less elastic (see *Physiology of the Muscle*), and these more quickly react upon the contents of the reservoir, and occasion in such cases frequent desire for micturition.

The important question now presents itself as to how the urine, during the quiescence of the bladder, is retained in this reservoir and does not escape through the orifice in the neck of the bladder. We all know that this is closed by a contraction of the vesical sphincter which surrounds the opening; but these muscular fibres are not very pronounced, nor can a muscle be kept in a continual state of contraction. The neck of the bladder is closed, because this is its natural form, like that of other and similar circular muscles; these obliterate the orifice which they circumscribe, when they are in a state of repose, and this is simply due to their elasticity.

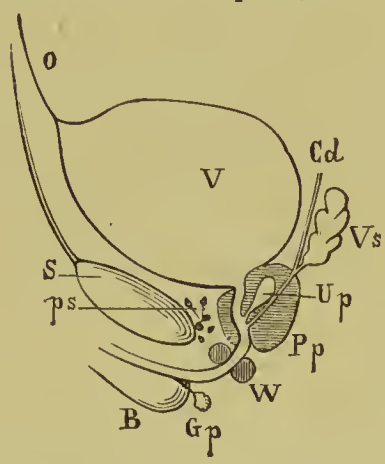


Fig. 129. — Bladder and organs of micturition.*

But so soon as some cause opposes this sphincter, it becomes powerless to prevent the passage, which the urine overcomes and rushes through. With women this orifice is differently arranged, and on a slight effort, or burst of laughter, several drops of urine may gush out. Certain arrangements and especial positions of the bladder, especially in man, are of such a nature that there exists no real orifice while the bladder is in a state of repose.

First, the axis of the bladder (Fig. 129) is by no means vertical, but almost horizontal (this organ rests upon the symphysis pubis, which has almost a horizontal position); the excretory

* S, Symphisis pubis. *ps*, Plexus of Santorini. V, Bladder. O, Remains of the urachus. P*p*, Prostrate gland. U*p*, Prostatic utricle. C*d*, Deferent canal. V*s*, Vesiculæ seminales, whose neck joins with the deferent canal to form the excretory duct, which may be seen going behind the prostatic utricle. W, The so-called Wilson's muscle (pubo-urethral band). G*p*, Cowper's gland. B, Bulb of the urethra.

canal, urethra, has first a position vertically downwards, then it turns and curves forwards; thus, this canal is liable to be compressed by the enormous distention of the bladder.

Again, the prostate gland (P*p*, Fig. 129) is a hard unyielding organ, being composed of glands, fibrous tissue, and muscular elements; this urethral opening penetrates and is encircled by this prostate gland in such way as to have its walls closed by contact. This forms the principal cause in man of the retention of urine during the inaction of the bladder. Should the prostate gland become hypertrophied, a still greater obstacle (too much so in old men) is made to the passage of urine, and becomes the cause of a pathological retention.

Finally, the flattening of the urethral canal and its closure by contact are influenced by the arrangement of the perineal fasciæ, the fibres of which press upon the sides of the urethral canal in their course from the ischium to the pubis; and a certain muscular and expulsive effort is required to overcome this constraint, and dilate the orifice.

It is not surprising in view of this explanation that the urine is allowed to accumulate in this muscular, dilatable, and elastic reservoir, and that no physiological act or contraction is required to prevent the exit of the urine; these conditions are simply mechanical and continue after death, since urine is often found in the bladder of the dead body.

When the walls of the bladder become too much distended by the presence of urine, we have said that a compression of the contents is produced by contraction of the smooth muscular fibres; this overcomes the elasticity of the neck of the bladder and of the prostate, and the urine passes into the bulbous portion of the urethra: here it comes in contact with a very sensitive mucous surface, the *prostatic mucous membrane*, which presides over a large number of reflex phenomena. It is owing to this contact of the urine with the mucous surface that we experience that peculiar sensation of a *necessity* or *desire for micturition*, and which we refer, in common with almost all other sensations of this region, to the fossa navicularis. If we pay no attention to this desire, a reflex irritation is produced, which is followed by the contraction of the constrictor urethræ, or urethral sphincter; the urine can then go no farther, and is even obliged to retrograde, on account of the contraction of the muscles on the anterior portion of the prostate, and so re-enters the bladder whose contractions have ceased.

These co-ordinated contractions, which occasion micturition, are made under the influence of the spinal cord, and particularly its lumbar portion. Budge has sought to fix the precise seat of this centre, and by experiments has placed the centre of innervation of the bladder in the fourth lumbar vertebra (in dogs and rabbits). Kupresson localizes this centre between the fifth and sixth lumbar vertebræ.

Sensibility of the prostatic mucous surface is very important, since this is the point of origin for the essential reflex action; loss of this sensibility is the cause of that form of incontinence of urine called *enuresis*, or nocturnal incontinence; this involuntary voiding of urine, as in similar cases of involuntary emission of feces, is explained by the *lack of sensibility of the mucous surfaces to the contact of excrementitial products, and in this particular case, the absence of a premonitory sensation of the desire to urinate.*

Some moments after the continued distention of the vesical reservoir, it reacts anew, and the urine proceeds to the prostatic portion of the urethra, where it stimulates anew the same reflex action, and so on. This explains the intermittent form of the desire for micturition. If these phenomena are often repeated, the reflex contraction of the urethral sphincter gradually loses its energy, and the urine tends to pass out through the urethral canal; hence the distress occasioned by resisting the desire to urinate. Thus it is seen that every time a true active resistance is offered to the passage of urine, this opposition is made, not by the sphincter of the bladder, but by the sphincter of the urethra, the *constrictor urethræ* muscle, which is the only one of these muscles which is striated or voluntary.[1]

If a sound be introduced into the urethra, as soon as its tip touches the mucous membrane of the prostatic portion, it will occasion a sensation similar to the desire to urinate; we refer this sensation to the other extremity of the urethra, simply because it is one of those associated sensations, examples of which we have already cited. (See *General Sensibility* and *Sensations*, pp. 79 and 388.)

When we yield to the desire, in spite of the absence of any obstacle on the part of the sphincter or constrictor urethræ, we cannot completely evacuate the contents of the bladder by the simple contraction of its walls. We must

[1] See Carayon, "De la Miction dans ses Rapports avec la Physiologie et la Pathologie." Thèse de Strasbourg, 1865, No. 814.

call in to our assistance the abdominal muscles, by means of which the abdominal viscera will press upon the bladder and increase the expulsive efforts of its walls. We close the glottis at the very beginning of micturition, and then the vesical contraction is sufficient for the expulsion of urine. But towards the end of micturition, in order to expel the last drops, a renewed effort is necessary: the lowest portion of the bladder being fixed and concave, we could not evacuate it completely, unless, by the aid of the abdominal muscle, we compress the upper against the lower portion of the bladder in such a way as to completely obliterate the cavity (Fig. 130); in man, then, the bladder when completely emptied (not so, however, with all animals) resembles a cup, and in this form it is seen in the dead body when this reservoir is completely empty.

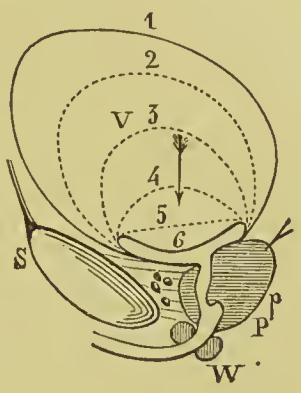


Fig. 101. — Diagram of micturition.*

As soon as the bladder has been emptied, the walls of the urethra are brought in contact and expel its contents; but when this canal is diseased and long-seated inflammation has destroyed the elasticity of the bladder, it is not thoroughly emptied, and the urine remaining in contact with the mucous surface, contributes to keep up the pathological condition.

II. GENITAL SYSTEM.

I. Male Organs of Generation.

The male organs of generation are composed of a *gland* (testicle) and a series of *excretory ducts*.

1. The *male gland*, the *testicle*, is the offshoot from an organ which is developed on the inner edge of the Wolffian body (see above); until the close of the second month this body presents no characteristic feature that would lead us to know whether it were a testicle or an ovary; but towards

* This diagram shows how the bladder is completely emptied.

1, Outline of the bladder when distended by a liquid. 2, 3, 4, 5, Represents the outline of the bladder when reduced by different intensities of its contractions. 6, Represents the outline when the abdominal muscles have adjusted the upper to the lower concave portion. The arrow indicates the direction in which the compression is made.

the third month, if it is to be a testicle, the canaliculi of the Wolffian body penetrate into its substance, there multiply, and become the *seminiferous tubuli.* At the same time the other portion of this body is atrophied, and the remaining portions with its excretory canal constitute, the former certain rudimentary organs (*non-pediculated hydatid* of Morgagni, *corpus innominatum* of Giraldès), whilst from the latter are formed: the excretory ducts of the testicle, *caput* or *head* and *body of the epididymis*, *vas deferens*, with numerous more highly convoluted tubes, which are the remains of the appendages of the Wolffian body; of these the most noteworthy and constant becomes the *vas aberrans.*

In this way the internal genital organs of man essentially spring from the Wolffian body; and form the testicle, vesiculæ seminales, and, finally, the ejaculatory canals; in brief, form all the organs that are comprised between the seminal gland and the genito-urinary sinus (prostatic portion of the urethra). The Müllerian duct (see p. 518) is completely atrophied in man; its only remaining trace is found in the two extremities that form the *pediculated hydatid* of Morgagni, and the central portion, which unites with that of the opposite side to form the *utriculus prostaticus.* We shall see that the Müllerian ducts represent the whole of the genital organs in woman, and especially form the *womb*, by the fusion of the two inferior portions of the duct on each side, in the same way that the prostatic utricle is formed in man: the *utriculus prostaticus and the uterus are homologous organs.*

A. *Testicle and its excretory canals.— Formation of the spermatic fluid.*

a. The seminiferous tubes of the testicle are sinuous tubes, tortuous like the tubes of Ferrein in the cortical substance of the kidney, and terminate at the posterior edge of the testicle in what is called the corpus Highmori (Fig. 131, C*h*), an eminence of compact fibrous tissue, wherein the seminiferous tubes cross (rete testis) to go to the excretory canals that form the epididymis.

The seminiferous tubes are quite numerous: 500 or 1000 have been counted in each testicle; they appear in the form of tubes with thin walls, almost entirely filled with polyhedral epithelium. This epithelium produces the spermatic fluid, whose secretion is temporary and not continuous. The testicle is inactive in childhood and old age. At the period of puberty, among the epithelial cells of these tubes, quite

voluminous seminiferous cells may be distinguished, *mother cells*, which result from the development of the primitive globules; these cells may be compared to the ovum of the woman: like the ovum these former cells are set free, have

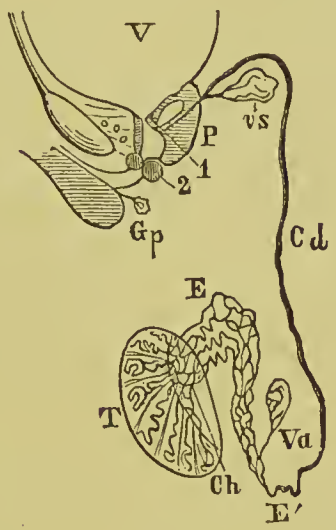


Fig. 131. — Genital system in man.*



Fig. 132. — Spermatozoids.*

an independent existence, and move about in a liquid caused by the moulting of neighboring globules; they are gradually chased through the epididymis and vas deferens. During their progress these cells, called *masculine ova* (*ovule masculin*, Ch. Robin),[1] undergo an active *endogenous segmentation*, and give birth to new globular forms which were contained in them: these are the *spermatozoids*, which are first seen as filaments rolled up in the

[1] See C. N. Demétriesco, "Etude sur les Ovules Mâles." Thèse de Paris, 1870.

* T, Testicle. *Ch*, Corpus Highmori, with the *rete testis*. E, Caput Epididymis, formed by the union of the seminiferous cones. E', Tail, *cauda*, or *globus* of the epididymis. *Va*, Vas aberrans. *Cd*, Vas deferens. *Vs*, Vesicula seminalis. P, Prostate, with ejaculatory canal; prostatic utriculus and veru montanum during erection (1). 2, So-called muscle of Wilson, in a state of contraction, obliterating the canal (at this moment the spermatic fluid can only accumulate in the prostatic portion of the urcthra between the points 1 and 2, whence it is propelled by the contractions of the preceding canals from E to VS). *Gp*, Cowper's gland. V, Bladder.

* *a*, *b*, Spermatozoids, taken from inside of the testicle. *c*, From the vas deferens. *d*, From the vesiculæ seminales.

globules of the mother cells, but which are set free when the latter are broken. These spermatozoids afterwards show a slight pear-shaped and flattened swelling (*head*), and a filiform appendage (or *tail*), terminating in a fine point (Fig. 132). Generally only the mother cells are found in the tubes of the testicle.

In those animals who enjoy the sexual functions only at certain periods of the year, the testicular secretion occurs only at those periods: they begin in man only at the age of puberty. Spermatozoids are never found in the spermatic fluid before the age of 16 or 17 years. They likewise are liable to disappear in old age. According to Dr. Girault, in man after the age of 55 years the head of the spermatozoids is broader and the tail is shorter; then comes a time when these species of tadpoles (*têtards*) have almost no tail: the head has absorbed almost the whole of this tail; a few movements may exist, but progression has become impossible: a few scattered ones in whom the tail remains have the power to go forward.

b. The spermatic fluid is perfected, or in other words, the spermatozoids are set free, only in the *epididymis* (Fig. 131, E) and in the canals (E′, C*d*): they then seem to be animated with very active movements of transportation, but, in reality, only represent the movements of vibratile cilia (see p. 189). Sometimes the head or the neck (union of the head with the tail) of the spermatozoid is encircled by a sort of collar or frill, which is the remains of the nucleus in which the spermatozoid was developed. Their movements become more noticeable in that spermatic fluid which is formed by the product of all the various glands, and as found in the ejaculatory ducts; the head moves to and fro by means of the impulsion received from the movements of the tail. No spermatic fluid is capable of effecting fecundation which has not these vibratile and moving filaments. This sperm, which has a tenacious whitish appearance, and a peculiar odor, contains an albuminoid substance called *spermatine:* this latter substance is not coagulated by heat, contains various salts (alkaline, chlorides, phosphates, sulphates), and, as physical or morphological elements, it also contains a large number of granulations, in addition to the spermatozoids, and likewise certain crystals which are analogous to the ammonio-magnesia crystals of the urine, but now considered to be altered and crystallized albuminates.

The sperm progresses through the epididymis (Fig. 131, E),

and the vas deferens (E′, C*d*) by means of the *vis a tergo* and by contractions of the muscular fibres in these canals. Venereal excitations singularly hasten its production and secretion; but when these excitations are repeated at too short intervals, the spermatic fluid has no time to be thoroughly elaborated, and hence the spermatozoids are often found in the ejaculated secretion still enveloped in their mother cells.

In its course from the testicle to the prostatic region, the sperm may turn aside into the *vesiculæ seminales* (Fig. 131, *v s*), which might be looked upon as a diverticulum of the vas deferens (spermatic duct) analogous to the *vas aberrans* (Fig. 131, V*a*), which are derived from the lateral cœca of the Wolffian body; but the function of a spermatic reservoir assigned to the seminal vesicles has never been perfectly demonstrated: most often there has only been found in this diverticulum a yellowish mucus, which apparently, in the same way as the prostate and Cowper's glands, gives to the sperm a more fluid character. The red globules of the blood are frequently found in the product of the seminal vesicles, especially when there has been no coition for a long time (Ch. Robin), but their presence need cause no alarm. The concretions which are found in these products are proved by their chemical properties to be formed of the nitrogenous concrete mucus. The seminal vesicles are not found in a large number of the lower animals, especially not the dog.

By peristaltic movements of the efferent system, the spermatic fluid is thrown along the *ejaculatory ducts* into the prostatic portion of the urethra; these ducts lead from the seminal vesicles and the termination of the vas deferens towards the posterior wall of the urethra (Fig. 131, p. 479). Then they pass through the posterior half of the prostate gland. In spite of the name *ejaculatory*, these ducts take no active part in this mechanical phenomenon: their thin walls, which are nearly devoid of muscular elements, would not allow of any active contraction. They serve only to conduct the sperm to the prostatic region, at which latter place its contact with the sensitive mucous surface excites a peculiar reflex action, the *ejaculation*, whose mechanism it is extremely difficult to study, but which is destined to project the male fecundating fluid into the female organs of generation. We shall first proceed to the consideration of a phe-

nomenon which precedes and renders this act more efficacious, viz. *erection.*

A. *Erection.*

The apparatus of erection is composed of the *penis*, *its cavernous body* and its *spongy body* (also the *bulb* and *glans*).

The object of erection consists in placing the urethral canal in the most favorable posture for the easy flow of the spermatic fluid, and for its transportation into the female organs of generation.

Erection is caused by a reflex action, whose point of origin is in the brain (imagination), and in most of the organs of the senses as well as in the sensitive surfaces; but the excitation of the mucous surface of the *glans penis* carries this reflex action to its highest degree. Indeed, the glans is furnished with numerous nervous papillæ which gives to it a special sensation, called *genital;* the excitation of this sensibility is the point of origin for that chain of acts which constitutes coïtus (erection, abundant secretion of sperm, excretion, ejaculation), just as the excitation of the fauces is the signal for the series of acts of deglutition. The dorsal nerve of the penis is the centripetal path for these reflex phenomena, which become impossible after section of this nerve, as attested by many repeated experiments on horses.

The question of the *mechanism of erection* is very complicated, and upon it there is little agreement: it has been demonstrated that this phenomenon essentially consists in an accumulation of blood in the texture of the cavernous and spongy portion of the erectile apparatus, but the embarrassment lies in the explanation as to how this blood is retained, and at so high a tension. Yet a few circumstances can clear up this study; thus it is admitted that an erection of the cavernous body is often independent of that of the spongy portion of the urethra, and can result without genital excitement, by a simple and mechanical opposition to the return of the venous blood; to this kind of erection belongs that produced when the bladder is distended with its fluid contents; this is followed by a compression of those venous plexus which are formed by an expansion of the dorsal vein of the penis (prostatic or plexus of Santorini, placed between the bladder and pubis *ps*, Fig. 129, p. 474). It is, then, probable that when the erection is really active it produces upon all the veins coming from the erectile parts a similar constric-

tion, either by contraction of the walls of the veins, or of the numerous layers of smooth muscles through which these veins pass before entering the pelvis (the middle layer of the perineal fascia are almost entirely composed of smooth muscular fibres); this would tend to arrest the blood in the texture of the spongy tissues, and so produce a pressure equal to that of the arterial blood.

In this way erection depends upon a reflex contraction which arrests the progress of blood in the veins; and, in fact, a pathological erection observed in dead subjects is associated with clots which fill the veins of the erectile tissue and extend to the veins of the pelvis; this would seem to prove that the compression occurs in the pelvic cavity.

Perhaps, also, vaso-motor paralysis (see p. 170, *Circulation*) has a certain influence upon the mechanism of erection, by allowing the erectile tissues to be distended with the afflux of blood; yet it is evident that if the path for the return of the venous blood should remain freely open, the vaso-motor paralysis would not be sufficient for the production of a true erection, and would only induce a more or less pronounced turgescence.

Professor Rouget[1] has established that in all cases there exists a dilatation of the small arteries; this same effect is observed in the hyperæmia of the ovary and the uterine mucous surface at the commencement of the act of menstruation, and is due, in his opinion, to the same causes as blushing and the reddening of the crest or comb of the male fowl called the cock. Finally, direct observation of the commencement of the erection of the organs of copulation, and the experiments of Eckhard on the paralysis of the small arteries of the cavernous and bulbous portions of the urethra after irritation of the *nervi erigentes;* both of these phenomena prove that paralysis and vascular dilatation are the initial phenomenon of all, even the most complicated kind of erection.[2]

But this phenomenon, though sufficient to prove the

[1] Ch. Rouget, "Recherches sur les Organes Erectiles de la Femme." ("Journal de Physiologie," Vol. I., 1858.) "Des Mouvements Érectiles." (Ibid., 1868.)

[2] Thus we can call to mind in view of erection all that has been said in regard to the physiology of the vaso-motor nerves. To this class of phenomena belong the theory of *active dilatation* of Schiff, and the *peristaltism of the blood-vessels* of Legros and Onimus (see *Vaso-motors*, pp. 173 *et seq.*).

simplest form of erection, or *turgescence*, would not suffice for those more complicated forms, as the erection of the bulb, ovary, and uterus; we must consider that the smooth muscular trabeculæ assist in the compression of the venous trunks; and it is equally certain that at the period of menstruation this permanent contraction of the uterine muscles, and those of the Fallopian tube, coincide with the application of the tube to the ovary, and accomplish this phenomenon. It is also true that the muscular trabeculæ of the spongy and cavernous tissue of the penis contract, after the dilatation of the small arteries. When this latter contraction does not occur, as in the dead subject, the size of the penis may be made enormous, and yet its rigidity be relatively incomplete.

Finally, in the erection of the organs of copulation of both sexes, the action of the extrinsic muscles is brought in play in order to complete its development; and in fact we know that an injection by the most forcible pressure will not produce a true erection unless preceded by ligation or compression of the large veins in the pelvis.

The centrifugal nerves which share in the function of erection have been classified in two groups, whose action is distinct and antagonistic (Rouget).

1. The cavernous and spongy nerves (branches of the large cavernous nerve given off from the prostatic plexus) are supplied from the grand sympathetic, and belong to that class of nerves which are provided with ganglionic corpuscles, whose irritation results in the paralysis of those arterial coats innervated by these nerve fibres (*nervi erigentes* of Eckhard).

2. Those nerves which go, without traversing the ganglionic corpuscles, to the muscles of the trabeculæ, and whose irritation is followed by contraction of the muscles which they supply (*nerfs uréthro-péniens*, *plexus latéral*); so also an irritation of the direct nerves (and without ganglia) which innervate the *erector penis*, *accelerator urinæ*, and the inferior transverse muscles, is followed by contraction of these muscles.

The *erector penis* and *accelerator urinæ* muscles may be called, from their functions, *true peripheral hearts;* their function consists in chasing the blood from the base to the free extremity of the penis. The former of these two muscles encircles the root of the corpus cavernosum, the latter the bulb of the urethra, and by their rhythmical contractions cause the erection of the penis from the base to its summit.

These muscles contract, in virtue of a reflex action (see above), influenced by the irritation of the *glans penis*, and at each contraction, we might almost say at each *pulsation*, of the *accelerator urinæ* muscle, the glans become more swollen and sensitive; and its papillæ being extended over a larger surface are more highly excited by the continued friction. When this sensation has reached its highest point, it occasions the reflex phenomenon of *ejaculation*.

C. *Ejaculation.*

Ejaculation is the termination of the venereal act, and its accomplishment is preceded by numerous accessory acts.

In the first place, by the fact of erection the urethral canal is dilated and open. This dilatation would naturally produce a certain aspiration or suction, and something must fill the canal which is transformed from a flattened to a cylindrical shape: it has been supposed that air is thus introduced, and this hypothesis would explain also those cases of *chancres* found in the interior of the urethra; and assuming that aspiration during coïtus has sucked into the canal a virulent liquid from the contaminated woman. Yet observation has shown that air does not rush in to fill the enlarged cavity, for in that case particles of air, in the form of bubbles, would be found in the excreted spermatic fluid; this latter phenomenon has never been observed. Cowper's glands, analogous to the salivary glands, which are situated amongst the striated and smooth muscular fibres of the perineum (middle fasciæ), and behind the enlargement of the bulbous portion of the urethra (Fig. 131, p. 479), secrete a fluid which would fill the vacuum in the canal; the excretory duct from these glands opens into the urethra at the union of its bulbous and spongy portions. The product of these glands thus would dilute the spermatic fluid, which primarily is quite thick. If a decided erection is not followed by the ejaculation of the sperm; at the cessation of the erection, when the canal returns to its original dimensions, there exudes from its anterior aperture (meatus) a clear and mucous substance, which simply is the secretion from Cowper's glands.

The other products of secretion, poured into the vacuum formed by the dilatation of the urethral canal, and whose mixture dilutes the sperm and so assists in its easy passage, come from the racemose *glands of Littre* and the *prostatic glands* (little glandular pouches radiating from the urethral canal in the posterior half of the prostate (Fig. 131, p. 479);

and are analogous to that from Cowper's glands and the seminal vesicles. The *utriculus prostaticus* does not apparently furnish a special liquid, nor take an important part in the function of reproduction, but is probably only a rudimentary organ.

The spermatic fluid, mingling with the product of the vesiculæ seminales by means of the contraction of these vesiculæ and of the efferent canals, arrives at the prostatic portion of the urethra; here its presence, by reflex irritation, sets up a mechanical action by which it is projected forcibly and with jerks outside of the canal; in other words, it is ejaculated. The forcible and jerky ejaculation has been generally attributed to the contractions of the *bulbo-cavernous* muscle, which has been named *accelerator seminis et urinæ;* but we must remember that this muscle is separated from the urethral canal by the interposition of the bulbous portion, rigid on account of its state of erection; and that moreover it is placed in front of the prostate, or in front of the place where the spermatic fluid has been poured in; and, consequently, it is difficult to understand how it can assist primarily in expelling the sperm, though it may possibly act ulteriorly in completing the ejaculation of the sperm, in that part which lies between the prostate and glans penis.

At the moment that the sperm is poured into the prostatic portion, this portion of the canal is isolated from the bladder on account of the erection of the *verumontanum* (Fig. 131), a little eminence situated on the posterior wall of the canal, and which in its state of turgescence is in contact with the anterior wall; this would then obstruct all communication between the bladder and the urethral canal, and we all know that micturition is impossible during the state of erection. On the other hand, the ducts, incorrectly called ejaculatory, open *in front of and at each side of the verumontanum*, so that the sperm can readily pass into the urethra, and fill up the whole prostatic portion; but it can go no farther, because at this moment the so-called Wilson's muscle contracts and obliterates the membranous portion (Fig. 131, 2). The seminal fluid then accumulates in the straight part of the canal comprised between the verumontanum and the urethral sphincter, or Wilson's muscle (Fig. 131, from 1 to 2); here it accumulates under a high pressure, because the contractions of the smooth muscles which pushed it there (efferent canal and seminal vesicles), though slow, are very energetic. It cannot pass towards the bladder owing to the obstruction offered by

the verumontanum; it cannot immediately escape along the canal on account of the contraction of the urethral sphincter. But this muscle cannot long maintain its state of contraction; it relaxes, and immediately, under the influence of the high pressure which it has acquired, the seminal fluid is precipitated, and forcibly precipitated; then the muscle again contracts and arrests the seminal eruption; again suddenly relaxes and so on, so long as the ejaculation continues. We see thus that the force of the ejaculation is due to the sudden relief of the high pressure, and the rhythm to the alternate contraction and relaxation of the urethral sphincter.

In this view it is seen that the integrity of the prostate is as important to the act of generation, as it is to that of micturition. It is here also the contact of the seminal fluid with the mucous surface which influences the intermittent and tetanic contraction of the urethral sphincter. So, also, disease of the prostatic mucous surface has a great influence over the function of generation, and may cause, either satyriasis, impotence, or seminal emissions. This explains the usefulness of cauterization (Lallemand) to counteract the last-named disturbance.

It is interesting to note the circumstances which favor the movements and vitality of the spermatozoids in the ejaculated seminal fluid. Cold water, the electric spark (Prévost and Dumas), and acid solutions destroy the spermatozoids; slightly alkaline and neutral solutions are favorable to and increase the activity of their movements. The vaginal mucus destroys them only when it is very acid; under ordinary circumstances the spermatozoids remain living for a long time in the vagina, and Percy has collected them in a state of activity at the neck of the womb, eight days after the last coïtus.[1] Finally, according to Godard, the menstrual blood increases the activity of their movements.

Moreover, the spermatozoids can live in pus, blood, and various other fluids. Sims has often seen conception take place even during severe suppuration of the neck of the uterus. According to Kölliker phosphate of soda is especially favorable to their activity.

[1] See Marion Sims, "Notes Cliniques sur la Chirurgie Utérine." Traduct. française, Paris, 1872.

II. Female Organs of Generation.

These organs of generation are composed of a *gland* (ovary), and excretory canals (Fallopian tube, womb, vagina, &c.), whose points of interest are represented, on one hand, as organs for copulation (vagina and its appendages), and on the other hand, as a place (womb) where the product of fecundation may be developed.

1. The ovary arises from that germ which, as we have learned, was placed on the inner border of the Wolffian body and remains unchanged until the close of the second month of embryonic life. We have also learned how this germ is developed into a testicle. When, however, it is destined to develop into an ovary, the peritoneal epithelium, which envelops the germ, sends offshoots or vegetations in form of *culs de sac* or pouches, which penetrate into the deeper portions of the organ (Fig. 133); these form true tubular glands (Fig. 133, 1, 2, 3); but soon the orifice of these tubular glands is obliterated (*id.*, 4, 5), and there remains only a little cavity (*id.*, 6) which is lined with epithelium and is completely closed. These very numerous cavities constitute the *Graafian vesicles* (Fig. 134); their epithelium is thus an offshoot from the peritoneal epithelium.

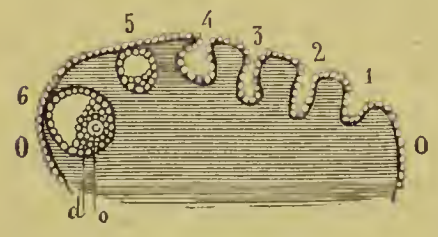


Fig. 133. — Development of the Graafian vesicle.*

2. The excretory canals are formed by the development of the *Müllerian ducts* (p. 478). The upper portion of these two ducts forms the Fallopian tube, which is free and ununited on either side; the lower portion unites with the corresponding portion of the opposite side to form the uterus, and an incomplete fusion of the two sides forms, in animals, the *bifid uterus* or double and independent wombs, as in the *rodents*. Thus is seen, as the opposite of what occurs in the development of the male organs of generation, that the Müllerian ducts develop into the female organs of generation, and the Wolffian body becomes atrophied; sometimes, and always in the cow, the excretory canal of the Wolffian body

* OO, Surface of the ovary, and its epithelium, which at 1 forms a deep pouch, a sort of tubular glandular structure: this gland is gradually more and more isolated at 2, 3, 4, 5; at 6 it is completely separated, and forms a cavity lined with epithelium, which is hypertrophied at one point (*d*, Proligerous disc), wherein one of the cells has become the ovary (*o*).

persists in a rudimentary state, and is known by the name of Gärtner's canal.[1]

The vagina alone has not its homologue in man; it seems to be a sort of intermediate territory between the internal and external organs of generation.[2]

The *external organs of generation* originate, as in the case of man, from a perineal cleft which is in connection with the mucous surface of the deep-seated organs; only, whilst this cleft or fissure is closed in man, and so forms a canal (membranous and spongy portion of the urethra) which opens only at its anterior and superior extremity (*meatus urinarius*); in woman this fissure remains open, its boundary being formed by two cutaneous folds (labia majora), which do not join together, but circumscribe what is called the vulvar opening. Thus it may be seen that generally all the genital parts in women have their homologue in man. The urethral canal of the woman corresponds to that part of the urethra of the man, which extends from the neck of the bladder to the *verumontanum* or *caput gallinaginis* (crista urethræ), upon the summit of which, and in front, opens the prostatic utricle or male uterus.[3]

A. *Ovary and ovulation.*[4]

To sum up, the ovary is an organ formed, in a physiological sense, of *culs de sac*, which become isolated and closed vesicles, and are lined with *globular* or *spheroid epithelium*. We shall find that there are three distinct kinds of epithelium in three grand divisions of the female organs of generation; viz., the globular form in the ovary, the vibratile columnar in the uterus, and, lastly, the tessellated pavement in the vagina.

The physiology of these organs shows that the epitheliums are the most important of their elements; with scarcely any activity in infancy and youth, at the period of puberty the

[1] See Follin, "Recherches sur les Corps de Wolff." Thèse Inaugurale. Paris, 1850.

[2] See A. Courty, "Maladies de l'Utérus, des Ovaires, et des Trompes. Notions Préliminaires." Second edition, 1870, p. 74.

[3] Kölliker, "Entwickelungsgeschichte des Menschen und der höheren Thiere." Leipzig, 1861.

[4] The importance of the ovarian function and its anomalies may be found by reference to Albert Puech, "Des Ovaires, de leurs Anomalies," in "Montpellier Médical." 1872 and 1873.

function of these epitheliums is suddenly developed; the ovarian epithelium gives the signal and ovulation ensues; the *epithelium* of the *uterus*, next, becomes very active either in the form of simple menstruation, or of gestation; lastly, the vaginal epithelium as well as its appendages (external genital organs) does not remain quiescent.

As the ovary is the seat of origin for most reflex and pathological phenomena we will commence our study with that organ.

The *ovisacs* or *Graafian vesicles* are formed of a little pouch of connective tissue, on whose inner surface a thick

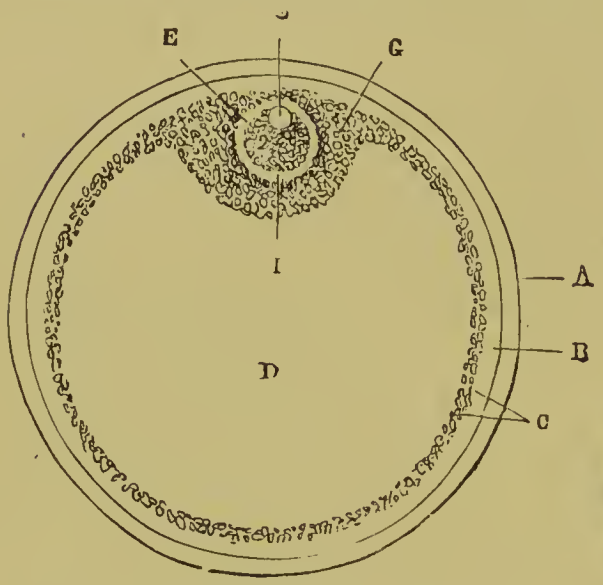


Fig. 134.
Graafian vesicle enclosing an ovum.*

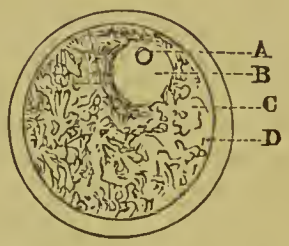


Fig. 135.—Ovum.†

layer of small globules are found (*membrana granulosa*, Fig. 134); at one point this layer is a little thicker and forms the so called *proligerous disc* (G). One of these globules (E) of the proligerous disc becomes developed to a considerable size, being summoned to a higher destiny than its companions, and forms the ovum, the most perfect type of the cellular condition (Fig. 135); the ovum attains a size of $\frac{1}{10}$ or $\frac{2}{10}$ of a millimetre, and may be visible to the naked eye.

* A, B, Fibrous layers of the vesicle. C, Membrana granulosa. G, Tunica granulosa or proligerous disc, with the ovum. 1, Vitelline membrane. 2, Vitellus or yelk. 3, Germinal vesicle of Purkinje.

† A, Nucleolus, or germinal spot. B, Nucleus, or germinal vesicle. C, Yelk. D, Vitelline membrane, or zona pellucida.

Sometimes two ova are found in a Graafian vesicle (Bischoff,[1] Davaine[2]). This ovum is composed of a cellular envelope or *vitelline membrane* (or *chorion*, D), having protoplasmic contents or *yelk* (*vitellus*) (Fig. 135, C); we must not, however, confound this yelk with the entire yellow part of a bird's egg; the latter contains the egg of mammalia, as its *tread* or *cicatricula*, and, in addition, a great mass of nutrient material, the yellow, properly so called; a nucleus or germinal vesicle (B), which contains inside a nucleolus or germinal spot (A), is always found in the vitellus.

Not all the Graafian vesicles of an ovary arrive simultaneously at this degree of development, nor do they contain all their ova in a state of maturity.

It is only at the commencement of the period of puberty, or, more correctly, at each menstrual period, that *one* or *two ovisacs* (Graafian vesicles) are perfectly developed. At this time one of the Graafian vesicles, usually that next the surface of the ovary, is swollen, its contents augment, and it becomes more marked; that portion of its wall nearest the surface of the ovary presses against this surface; at this point occurs an arrest of nutrition, and consumption of its own walls; this condition, assisted by an increasing swelling of the central portion of the ovary (*stroma or spongy portion of the ovary*) readily induces a rupture of such a nature that the contents of the ovisac escape, bringing out the ovum with the *debris* of the proligerous disc. Usually this is the most favorable moment for fecundation of the ovum by the arrival of the spermatozoids, if, perchance, these latter have been introduced into the female genital organs; but whether the ovum is, or is not fecundated, the appendages of the uterus act, in a mechanical point of view, almost in the same manner.

After the expulsion of the largest part of its contents, the Graafian vesicle closes again and undergoes a cicatricial healing of its ruptured envelope, leaving but a slight trace of its rupture; it has also a yellow color received from the blood pigment, arising from a slight hemorrhage which accompanies

[1] Bischoff, "Traité du Développement de l'Homme et des Mammifères," suivi de l'histoire du développement de l'œuf du lapin. Translated from the German by A. J. L. Jourdan. Paris, 1843.

[2] Davaine, "Mémoires sur les Anomalies de l'Œuf." Paris, 1861, 8vo, with illustrations.

its rupture. It is a most wonderful fact that, if the ovum does undergo fecundation, arrives in the uterus, and gestation occurs, there is produced in the ovary, by some mysterious and sympathetic reflex action, a hypertrophied evolution of the ruptured ovisac; to this hypertrophy an atrophy ultimately succeeds (at the close of pregnancy), which gives rise to a cicatrix analogous to the preceding, but much larger and more enduring. These cicatrices are called *corpora lutea* (corpus luteum, a yellow body): the first are called *yellow bodies of menstruation*, or *false yellow bodies;* the others are called *yellow bodies of fecundation* (of pregnancy), or *true yellow bodies.*

B. *Fallopian tube, womb, and menstruation.*

The ovum expelled from the ovary then falls outside that organ; it may fall into the peritoneum and there disappear, and, in case of fecundation, may there undergo a development (peritoneal pregnancy);[1] but this is not the normal course: in the physiological conditions, *ovulation* is accompanied with particular phenomena which cause the ovum to fall into the fimbriated extremity of the *Fallopian tube* or *oviduct.* The *Fallopian tube* is a movable, contractile, and erectile organ. The contractility of this tube and that of the smooth muscular fibres which are found in the *broad* and *ovarian ligaments*, must favor the application of the orifices of the Fallopian tubes to the ovary (Ch. Rouget); yet, its erection has also some influence in this act, since there is sufficient erectile tissue arranged in such a manner that when in a state of turgescence the fimbriated extremity of the Fallopian tube would be made to embrace in its cavity the whole ovary. The ovum thus falls into the end of the Fallopian tube, whence, by means of the movements of the ciliated epithelium, and on account of the peristaltic contractions of this oviduct, it is passed along into the womb; at this latter place it sets in action certain phenomena if the ovum has been fecundated, or if it is non-fertilized it is thrown off with the catamenial or menstrual flow.

It has been recognized, in fact, that the fall of the ovum coincides almost exactly with the menstrual period[2] (every

[1] See Th. Keller, "Des grossesses Extra-utérines (avec deux observations de Kœberlé). Thèse de Paris, 1872, No. 157.

[2] See Pouchet, "Ovulation Spontanée et Fécondation." Paris, 1847.

28 days on the average). The fall of the egg, consequently, is periodical; this phenomenon is accompanied with other accessory phenomena, called *molimina menstrualia*, which consist of: a congestion of the spinal cord, pain in the lumbar region, phenomena of eccentric sensibility, pains at the surface which should be referred to the spinal cord; finally, the uterine phenomena, *menstrual hemorrhage*, *catamenial flow*.

The *catamenial flow* should be carefully examined, as we shall discover a phenomenon which is essentially epithelial. The uterus, a muscular organ to be sure, but whose muscular element displays its important function only during or at the close of gestation, presents a cavity which is lined with a mucous surface; this lining is really only a *vibratile columnar epithelium*, almost immediately attached to the muscular element, with scarcely any substratum of connective tissue like the corium in the skin. This epithelium is quite abundant, is endowed with a good deal of activity, and forms by its deep vegetations, tubular glands analogous in appearance to the glands of Lieberkühn, and which are imbedded in the muscular walls; we shall see that at the moment of fecundation this epithelium forms enormous papillary vegetations which give origin to the *decidua:* in pathology it is frequently the source of a large number of uterine neoplasms. More remarkable, however, than these is the fact that this epithelium is subjected to a sort of monthly *moulting*, exactly coincident with ovulation; a similar fact is observed in the *heat* or *rutting* of female mammalia. Now as this epithelial lining protects or covers the uterine muscle, which is quite vascular and even erectile, it happens that the epithelial shedding exposes a large number of little vascular canals; which burst under the influence of the general turgescence of the organs at this moment, and occasion, especially in woman, a more or less abundant hemorrhage. Thus though the hemorrhage would seem to be the most important phenomenon, it is none the less true that the very essence of menstruation is an epithelial moulting, sympathetic with the epithelium development in the ovary, and whence results the shedding of the ova or ovulation.

It is unnecessary to state that at this period of the menstrual hemorrhage the vessels themselves exercise no especial function: at this time there are certain modifications of the vaso-motor innervation that, unless the blood is thrown off from the uterine surface, the hemorrhagic flux will be accom-

plished by other vessels. Of this nature are the nasal, pulmonary, and intestinal hemorrhagies, which sometimes occur in women at the catamenial period. Recently a case has been reported (Tueffard, Un. Med., 1872) of a woman whose breasts every month were the seat of a painful swelling, followed by a dribbling at first of serous fluid, then bloody, which condition lasted during eight days.

Vagina. — The pavement epithelium of the vagina and of the neck of the womb is not inactive during the phenomenon of menstruation: an epithelial desquamation, upon a smaller scale, occurs in these places also, in consequence of which occurs a thick whitish product. In certain frequent and pathological conditions this desquamation is permanent, and forms a white or yellowish discharge, commonly known as "whites," or *leucorrhœa*, from the vagina, and especially from the neck of the womb.

The external genital organs likewise give off an analogous epithelial desquamation, but more nearly resembles a sebaceous product, or more like the *smegma præputialis*.

The vagina and the external genital organs especially serve for the purposes of copulation, whose object is *fecundation*.

III. FECUNDATION AND DEVELOPMENT OF THE FERTILIZED OVUM.

I. Fecundation.

Fecundation is the result of the encounter of the *ovum* and *spermatozoids*. We know that the male organ is arranged for the ejaculation of sperm. The female organs destined to receive this are:

a. External genital organs, which have erectile organs (*bulbus vestibuli seu vaginæ*, and *cavernous body of the clitoris*), rudimentary but analogous to those of the man; these organs, and especially the region of the clitoris, analogous to the glans penis, are the principal seat of voluptuous venereal sensations: —

b. The vagina, at the entrance to which (between the *labia minora* and the *carunculæ myrtiformes*), open on either side the excretory duct of the two *glands of Bartolini*; which are analogous, both from their secretion and product, to Cowper's glands, which we studied in the male. Their product seems to lubricate the entrance to the vagina. These

glands are interesting in a pathological point of view; here is the seat in woman of an inflammation analogous to gonorrhœa in man: in these cases there never vaginitis: *gonorrhœa* in woman should be translated *Bartholinitis.*

The vagina is essentially the organ of copulation: its ridges and transverse rugæ excite to the highest state the sensibility of the glans and induce the reflex phenomenon of ejaculation: in the vagina are let loose the spermatozoids. The condition of its mucous surface influences the vitality of these fertilizing elements: an acid secretion is fatal to these vibratile filaments; whilst an alkaline mucus, like the ordinary product of the pavement epithelium of the neck of the womb, is eminently favorable to the vitality and movements of the spermatozoids (see p. 567).

It is not necessary that the voluptuous sensations which in man accompany the *ejaculation* of sperm during coïtus should exist in women for the induction of *fecundation;* the sole conditions, fulfilled by the external organs of generation in the woman, is to allow the introduction of *seminal* fluid into the vagina and to hold it there. The hymen, which always presents a perforation of variable form (semi-lunar, horse-shoe, annular, or bilabial hymen), opposes no obstacle to this introduction, and ordinarily the hymenal membrane is broken at the first contact; but oftentimes this membrane presents a very defined sensibility, which, set in action by the slightest touch, induces by reflex action an energetic contraction of the vaginal sphincter, a contraction which is accompanied by violent pain, and opposes an obstacle to coïtus.

This curious, in its physiological aspect, phenomenon has been examined by Mar. Sims (of New York), under the name of *vaginismus;* quite reasonably, Sims compares vaginismus with blepharismus (nictation), or spasmodic and painful contraction of the orbicular muscle of the eyelids, accompanied with an extreme sensibility to light, or photophobia. This surgeon has, moreover, demonstrated that vaginismus cannot be abolished nor modified by forcible or gradual dilatation, so long as it is concerned with the origin of the reflex irritation, that is, with the hymen or its remains (caruncule myrtiformes); but that excision and cauterization of these sensitive membranes (especially on their external surface) cause an immediate disappearance of these spasmodic contractions, which were the cause of the hyperæsthesia.

On account of the fact, that the aperture of the meatus urinarius of the glans during erection has a vertical, and that

of the neck of the womb a transverse, position, it is possible that the spermatic fluid should be thrown directly into the uterus. This passage would be more readily accomplished by the state of erection of the uterus and its neck, on account of the opening being thereby enlarged; it has been said that this erection would dilate the cavity and thus induce, on the part of the womb, a true aspiration of the sperm. However, direct observation in animals (the rabbit) shows that the spermatic fluid is only thrown into the vagina.

According to the researches of Arm. Després (Académie de Médecine, Decembre, 1869): "The neck of the womb is furnished with racemose or tubular glands placed in a portion of the muscular tissue of the womb, like the prostatic glands in the midst of muscular fibres in the prostate. These glands secrete a clear, viscous, and albuminous fluid, analogous to the prostatic fluid, which flows from the neck in an intermittent manner, and produces the *ejaculation* in the woman. This fluid slowly flows from the neck of the womb and remains upon the *os uteri*, and in the cavity of the neck: *this ejaculation in the woman is destined to provide a vehicle for the zoosperms, and allows them to arrive with certainty into the neck of the womb.*[1]

Under these circumstances it is incontestable that the peculiar movements of these vibratile elements themselves form the essential condition of their meeting with the ovum: occasionally it is only necessary to deposit the spermatozoids at the vulvar aperture, and these, by their own movements, seek the ovum by following the vaginal passage, through the neck and the body of the womb, and, finally, the Fallopian tube. It is known, also, that a small quantity of sperm from the male frog, deposited at the end of one of the long strings of eggs which these animals lay, has fertilized even the last ova at the other end of the chain.

The encounter of the spermatozoids with the ovum, or *fecundation*, occurs even in the ovary, or at the fimbriated extremity of the Fallopian tube, as has been proved by peritoneal or tubal conception and pregnancy.

The phenomenon of fecundation results from the penetration of the spermatozoids into the substance of the ovum, where they dissolve and disappear. It is difficult, on account

[1] Arm. Després, "Etudes sur quelques Points de l'Anatomie et de la Physiologie du Col de l'Utérus." ("Bulletin de l'Acad. de Médecine, 1869, Vol. XXXIV. p. 1131.)

of the thickness of the vitelline membrane, to comprehend this penetration; though in a number of the lower animals pores or canaliculi have been observed, which might afford a passage for the fecundating element (*micropyle*).

In a recent work[1] on fecundation and development of the ovum in rabbits, Weil has assured himself that spermatozoids do penetrate into the very substance of the ovum. He also states that they preserve their active movements for several hours after their passage through the vitelline membrane. He has not only seen them during the separation of the cells from the vitellus after its segmentation, but even inside the protoplasm of the vitelline cells. At this latter place the spermatozoids lose their outline and disappear. An examination of all the evidence presented would apparently prove, that fecundation (conception) essentially consists in a fusion of the spermatozoid with the female element. This view is also supported by the comparative study of fecundation in the lower vegetable life (in the *spirogyra*, for instance).

Under the exciting influence of the fecundated or fertilized ovum in its course of development, the uterine epithelium is the seat of wonderful changes. The mucous tissue forms large pouches, and, so soon as the ovum comes into the womb, it is lodged in a valley formed by two of these pouches or villi; then these latter grow in every direction and finally completely enclose the ovum, so that a perfect envelope called the *caduca* (Fig. 136, *c*, *ee*, *f*, *k*), or *membrana decidua* is formed around it. The whole of the lining mucous surface of the uterus is called the caduca; that portion which lines the uterus is called *uterine caduca* or decidua vera (Fig. 136, *c*); that which forms a complete envelope of the egg is called *fœtal caduca* or *decidua reflexa* (*ee*, *f*); that surface of this decidua reflexa which is continuous with the first-named (that is, the very point of attachment of the egg to the uterus) is called the *caduca serotina*, or decidua serotina (Fig. 136, *ee*), in accordance with false ideas formerly held in regard to its mode of development. The *placenta* (Fig. 136 and 143) is formed near, and partially at the expense of, the *caduca serotina*.

The muscular portion of the uterus also undergoes hypertrophy, and forms new (smooth) muscular elements, simultaneously with the enlargement of preëxisting fibres. Finally, the vessels partake of this increase of development, as increased

[1] C. Weil, in Stricker's "Medic. Jahrbücher, 1873.

vascularization by arteries and veins is required for the nutrition of the new being undergoing process of development. An increase of the muscular elements is required for the process of *expulsion* (parturition, or labor) of the new being when perfectly developed (fœtus at full term of pregnancy). It is sufficient to state that this act, like all those heretofore

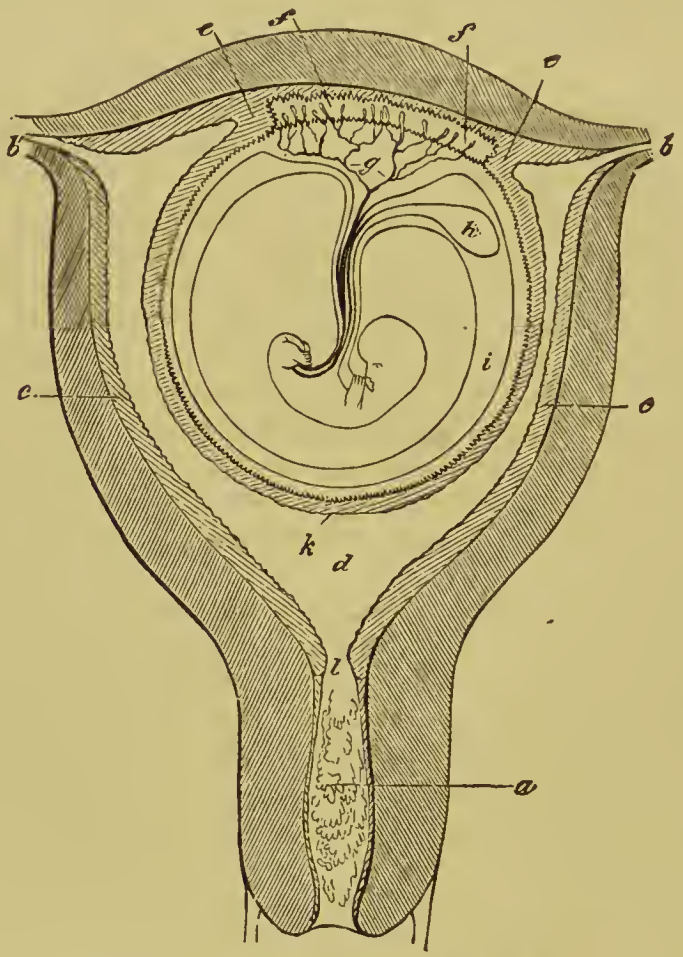


Fig. 136. — Womb, egg, and membranes.*

studied, is under the influence of the nervous system ; we shall see here also reflex phenomena analogous to all those which concern expulsion and excretion. The point of origin for these phenomena is normally in the uterus; but various excitations

* Vertical section of the womb, containing a developed egg or ovum. *a*. Neck, filled with a gelatinous plug. *bb*, Orifice of the Fallopian tubes. *cc*, Membrana decidua vera. *d*, Uterine cavity, almost entirely filled with the ovum. *ee*, Where the decidua vera is continuous with the decidua reflexa. *f*, Caduca *serotina* or *placenta*. *g*, Allantois. *h*, Umbilical vesicle and its pedicle in the umbilical cord. *i*, Amnion. *k*, Decidua reflexa and chorion.

can occasion it in parts even at a distance from the pelvic organs. Certain investigations on rabbits (W. Schlesinger) show that excitations of the central portion of the spinal nerves induce uterine contractions; and the same effect has been caused by excitations of the central portion of the pneumo-gastric; moreover, clinical observation has shown that a mechanical irritation of the breasts favors uterine contractions.

II. Development of the Fecundated Egg.

The result of fecundation in the ovum consists of *segmentation of the vitellus.* We commenced our studies with the *globular proliferation* (p. 10); this is a type of one of the manifestations of the general characteristics of the globules, consisting of segmentation and reproduction. Simple segmentation can sometimes occur without fecundation; but, generally, the presence of the spermatozoids seems to set in action a physiological excitation which induces the division of the vitelline protoplasm; in every case of segmentation of the unfertilized ovum, this segmentation does not extend very far, and never forms the *blastodermic membrane.*

I. *Envelopes of the embryo, respiration, nutrition.*

These envelopes vary according to the period of the development of the embryo; and, since they are the *seat* of the *exchanges* between the fœtal organism and its external medium (maternal organism), the manner in which these exchanges (nutrition and respiration) are performed depends upon the different periods of the embryonic life.

First, After the fecundated egg has traversed the tubal canal, and segmentation of the vitellus has occurred, the egg has no other envelope than its *vitelline membrane* (see Fig. 137) upon whose surface little homogeneous villi are developed; these constitute the *first chorion* (Fig. 137, 1). By the process of osmosis and imbibition, the albuminous liquids in the Fallopian tube and the uterine cavity pass through this membrane, and are borne along with the segmentation of the vitellus.

Secondly, when the segmentation is completed, and the blastoderm is formed, the relations between parent and embryo are more regularly established by the formation of new envelopes and a *placenta;* but, in the human species, at this transitional period, there is established a mode of nutri-

tion, which is more durable than in the ovipara, which has its source from an organ called the *umbilical vesicle;* finally, when the body of the embryo is developed it is protected in

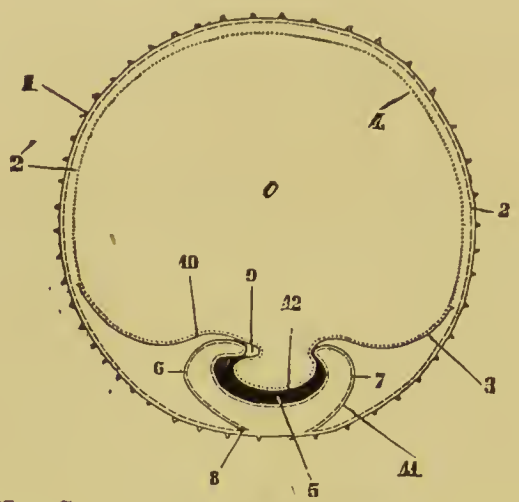


Fig. 137. — Commencement and development of the egg.*

a pouch or diverticulum, *amnion*, whose fluid contents ward off sudden compressions.

Umbilical vesicle. When the blastoderm (see p. 17) is formed around the egg, by its simple nutrition, as above shown, it attains a considerable size, from the fact that its interior forms a cavity, whilst the division of the blastoderm into three folds (*u*, *a*) becomes more pronounced at that place in which the body of the embryo will be formed (Fig. 138). But as the embryo becomes gradually developed, the circular region, by which it forms a part of the common blastodermic vesicle, gradually recedes (from 9 to *al*, Fig. 139) in such a manner, that soon the primary cavity becomes divided into two secondary cavities (Fig. 137, *o* and 12), one of which forms a portion of the embryo (12), its future intestinal cavity (see pp. 184, 232, and 424), and the other forms a vesicle placed above the ventral portion of the embryo (Fig. 137, *o*), the *umbilical vesicle*, which communicates with the intestine only by a canal called the omphalo-mesenteric duct (Fig. 139 and 140); the place at which this

* 1, Vitelline membrane. 2, External layer of the blastoderm. 3, Middle layer. 4, Internal layer of the blastoderm. 5, Form of the embryo. 6, Cephalic fold of the amnion. 7, Caudal fold of the amnion. 8, Extremity of the cephalic fold, which tends to join the corresponding extremity of the caudal fold. 9, Point for formation of heart. 10, Umbilical vesicle, yolk sac. 12, A portion of the internal fold of the blastoderm, from which the intestine will be formed.

duct is continuous with the intestine is the *intestinal umbilicus*, and the walls of the body which close around this duct form the *cutaneous umbilicus*, or *navel* (see p. 231, Fig. 64).

The umbilical vesicle contains a fatty albuminous fluid which represents all the extra-embryonic portion of the vitellus. This liquid serves for the nutrition of the mammalian fœtus until the placenta is developed. The absorption of the fluid of the umbilical vesicle is accomplished by a system of blood-vessels (*primary circulation*, see farther on),

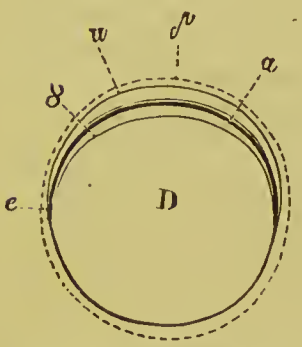


Fig. 138. — Blastodermic vesicle.*

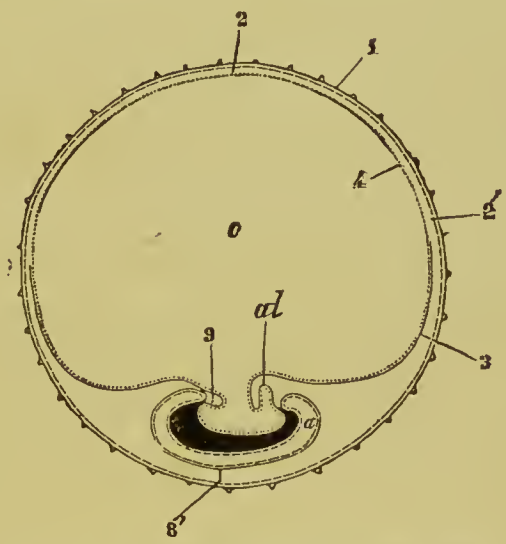


Fig. 139. — Egg with its umbilical vessel fully developed.†

which are developed in the external wall of the vesicle (*omphalo-mesenteric vessels*); these absorb the contents of this cavity by the medium of the internal epithelial surface of the vesicle, just as in adult life the mesenteric vessels (*vena porta*) absorb the contents of the intestinal canal by the medium of the villous epithelium, (and indeed fine vascular villi are often found on the internal surface of the umbilical vesicle).

* D, Yellow, δ, Vitelline membrane. *u*, Membrane at the external layer of the blastoderm. *α*, Middle layer. γ, Internal layer.

† 1, Vitelline membrane. 2, External layer of the blastoderm. 3, Middle layer of the blastoderm. 4, Internal layer. 5, Body of the embryo. 6, 7, 8, 9, As in Fig. 137. *o*, Umbilical vesicle. *al*, Allantoid pouch or protuberance. *a*, Amniotic cavity.

In this Figure, as in Figs. 137, 140, 141, the interrupted lines show the parts belonging to the internal layer of the blastoderm; the black lines belong to the middle layer; the dotted lines belong to the external layer.

Yet, the existenee and funetions of the umbilical vesiele, or yolk sae, do not eontinue for any great length of time in the mammalia. The nutritive pabulum enclosed by it is not large; even at the fourth week the umbilieal vesiele begins to atrophy, and towards the fifth only a traee of it remains (Fig. 142). In the ovipara, however (espeeially in birds), the umbilieal vesiele lasts mueh longer, and plays a more important part in the nutrition of the chiek; it eontains the *yellow substance*, a provision whieh is suffieient for the development of the ehick in the egg, and feeds it even after the ehieken is hatehed, but at that time it is enclosed inside the abdominal eavity, until the ehieken is able to feed himself.

Amnion. As soon as the umbilieal vesicle and the body of the embryo have been eompletely separated by the strangulation that we have already studied (intestinal and eutaneous umbilieus), the distinetion between the three layers of the blastoderm beeomes more and more eomplete, and the external one gives rise to a partieular formation, the *amnion* and seeondary *chorion*. In faet, as soon as the eutaneous umbilieus is formed, and at the same point, the external fold (eutaneous) of the blastoderm extends in sueh a way as to surround the embryo, and forms two lateral layers which tend to unite at its dorsal region, forming at the two extremities two hood-like folds (*cephalic* and *caudal*, Fig. 137, 6, 7) whieh eover its eaudal and eephalie portions. Only the middle portion of the back of the embryo remains uneovered, but soon these folds and layers by proeess of development unite (Fig. 137, 8), until the only opening (*amniotic umbilicus*, Fig. 139, 8) is eireumseribed and eompletely elosed. From this time the embryo is enelosed in a eavity, *amniotic cavity* (Fig. 139, *a*), in whieh it is suspended in the ambient fluid, *amniotic fluid*, given out from the walls whieh form this eavity.

The internal surfaee of the amniotie eavity is formed by that entire portion of the external layer of the blastoderm, which has been isolated from the rest of this fold by the sueeessive hood-like covering of the embryo and the union of the amniotie umbilicus. This surface is eovered by an epithelial layer given off from a layer of embryonie eonneetive tissue (from the middle fold), in which smooth muscular fibres may be seen (Fig. 140, 141, dark and dotted lines). On aeeount of this formation the rest of the external fold of the blastoderm is henceforward completely isolated from the body of the embryo, and forms an extended envelope sub-

jacent to the primary chorion (to the vitelline membrane), and encloses all the appendages (amnion, fœtus, umbilical vesicle). This extended envelope then undergoes a peculiar development; pushed gradually against the vitelline membrane, it is duplicated (Fig. 137, 2, and Fig. 139, 2, dotted lines), induces absorption of the latter, is substituted for it, and thus becomes the most external fold of the egg; in its turn it presents little protuberances, and so forms the secondary chorion (Fig. 140, 2′). This second chorion is no more vascular than the first; up to this time the fœtus obtains its nutrition from the maternal organism only by imbibition, or receives it by means of the nutritive provision of the yellow (umbilical vesicle). But the development of the second chorion allows the establishment of a definite centre of exchange between the mother and embryo, by the formation of the *allantoïs*, one part of which will form the placenta.

Thirdly, the allantoïs is a pouch or protuberance from the inferior part of the intestinal canal (see p. 139, *al*, and Fig. 124, p. 458). When this pouch appears (Fig. 139, *al*), the amniotic cavity is so much developed that it surrounds the entire fœtus, and encloses the pedicle of the umbilical vesicle,

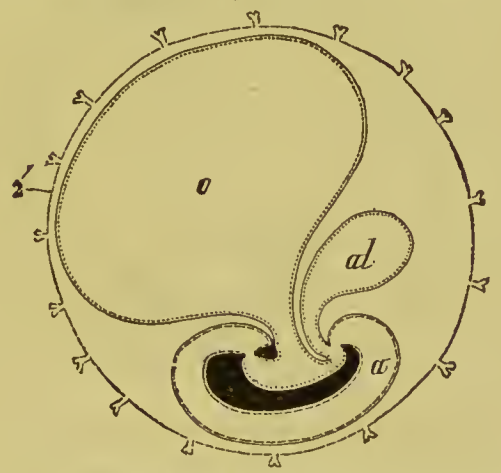


Fig. 140. — Umbilical vesicle and development of the allantoïs.*

in such a way as to form a cord by which the fœtus is suspended in the waters of the amnios. The allantoid protuberance insinuates itself in this cord (Fig. 140, *al*), pushes through and places itself by the side of the pedicle of the umbilical vesicle (omphalo-mesenteric duct), and then comes in

* *o*, Umbilical vesicle. *al*, Allantoïs. *a*, Cavity of the amnios. 2′, Second chorion.

contact with the deep-seated surface of the second chorion, which we have just studied. It extends over and substitutes itself for this surface, or, at any rate, penetrates the whole

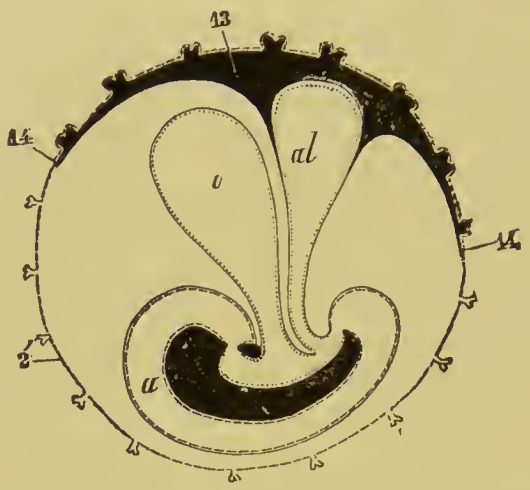


Fig. 141. — Development of the allantoïs and third chorion.*

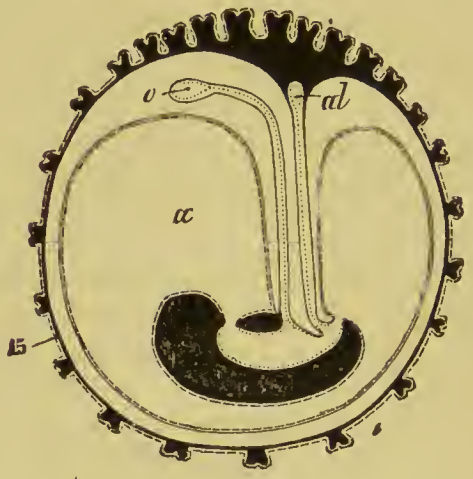


Fig. 142. — Third chorion or vascular chorion.†

of the outside of the egg between the external surface of the amnios and the internal surface of the chorion (Fig. 141, 13,

* *o*, Umbilical vessel in process of atrophy. *al*, Allantoïs. 13, 14, Allantoïs extending upon the internal surface of the second chorion. *a*, Cavity of the amnion. (Kölliker, "Entwickelungsgeschichte.")

† *a*, Amniotic cavity, well developed. *o*, Umbilical vesicle, almost completely atrophied. *al*, Allantoïd vesicle, properly speaking. 15, Its vascular villi completely developed, and forming the third chorion or vascular chorion around the egg (see explanation of Fig. 139 for the distinction of the dark, interrupted, and dotted lines). (Kölliker, "Entwickelungsgeschichte.")

14). In fact, the allantoïs, primarily vesicular, spreads into a membrane which is filled with villi, which latter penetrate into the villi of the second chorion. These villi of the allantoïs are vascular, and, uniting with the second chorion they form an enveloping membrane of the ovum, which definitely replaces the second chorion (Fig. 143, 15), and differs from the latter by the fact that its membrane is vascular and consequently capable of directly seeking by means of a regular circulation (second circulation) the nutritive elements supplied by the mother, and strained through the *decidua*, whose formation we have previously studied (see Fig. 136). This is what authors call the *third* or *vascular chorion*, or that membrane formed by the allantoïs, which afterwards becomes the most external of the proper envelopes of the egg, and which forms a covering for the remainder of the second chorion (Fig. 142, 15).

But these formations from the allantoïs last only for a short time, especially in the human fœtus. We have already learned that those portions of the allantoïs which are nearest the fœtus form successively the bladder and urachus (see p. 460); the other portion, from which the third chorion is formed (Fig. 142, 15), is provided with vessels only on the parts which correspond to the *membrana decidua serotina* (see p. 497); everywhere else the vascular loops of the villi undergo atrophy, and become the seat of no further transformations at these points until the birth of the fœtus (Fig. 143).

The envelopes of the perfected ovum are everywhere the same except at the placental attachments. Proceeding from the outside towards the interior are (Fig. 143): first, the decidua, or rather deciduæ (see p. 497), since, by the acquired developments of the egg, the decidua reflexa is in contact with the maternal decidua, or decidua vera (c, Fig. 136), and since these two membranes are not distinct from each other; however, they may be separated by a dissection, and often a certain amount of fluid may be found between the membranes (*hydroperion* of Velpeau) (21 and 23, Fig. 143); next comes the chorion (fusion of second and third chorions, 19, Fig. 144), the cells and villi of which, after the disappearance of the vessels, are united and fused in such a manner as to form a homogeneous membrane, which is more or less granular and interspersed with nuclei (Robin); third, a layer of irregular cells, which are the remains of the allantoïd body, is formed below the chorion; these have a stel-

late form, placed among a few connective fibres, and float in a semi-fluid substance ; this is the *magma reticulata* of authors ; lastly, comes the amnion which forms the *amniotic pouch* or *diverticulum*, and contains the amniotic fluid (Fig. 143, 18). The structure of the amniotic membrane recalls that of the

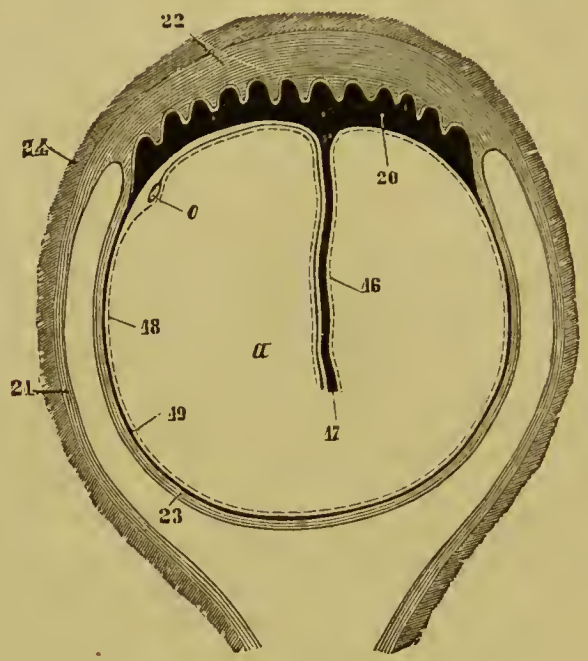


Fig. 143. — Envelope of the perfected ovum, — placenta.*

skin, with which it is continuous and whose origin it shares (external fold of the blastoderm) ; in fact, it is composed of an epithelial layer of pavement cells and a sort of dermis, formed of cellular tissue, which contains some smooth muscular elements.

Placenta, Nutrition of the Fœtus. — The essential office of the allantoïs consists in the formation, at the point where the villi still exist and which also have an exaggerated development (at the *decidua serotina*), the principal organ for the nutrition of the fœtus, viz., the placenta. In fact, at this place the villi of chorion and allantoïs (*chorio-allantoïd villi*) are developed, spread out in every direction (*placenta frondosum*), and ramify in the membrana serotina (Fig. 143, 22),

* *a*, Amniotic cavity (the body of the fœtus is not represented ; at 16 the umbilical cord, cut at the point of attachment to the umbilicus at 17). *o*, Remains of the umbilical vesicle. 18, Amnion. 19, The definite chorion. 20, Placental fœtus. 21, Mucous layer, or uterine caduca. 22, Maternal placenta. 23, Fœtal caduca, or membrana reflexa. 24, Muscular tissue of the uterus.

which here undergoes an hypertrophy; it is moreover characterized by the presence of both vascular and ramified villi. These villi originating on either membrane are joined together, interlace, and, finally, form the more or less circular and apparently compact cake, which becomes the centre of exchange between the maternal and fœtal organism (Fig. 143, 20).



Fig. 144.—Diagram of the placental vessels.*

An idea of the method of interchange between the mother and fœtus is represented by a diagram in Fig. 144. The fœtus receives and rejects the nutrient materials by means of an osmotic interchange through the capillaries of each villus; this constitutes nutrition and respiration.

The fœtal respiration is effected by means of the placenta; we have already spoken of this form of respiration (see p. 324). The necessity of placental respiration is, moreover, supported by the serious accidents which result from suppression of the placental functions. When the circulation of the cord which unites the placenta to the fœtus (see *fœtal circulation*) is interrupted, the fœtus perishes, not so much through want of nourishment, as from a true asphyxia; at birth pulsations in the cord cease only when the infant respires through the lungs, because then the new method of respiration definitely replaces that which has been accomplished by the utero-placental connection.

The *nutrition* of the fœtus during the placental portion of its life consists of an interchange of materials between the fœtal and the maternal blood through the placenta. Moreover, the relations which combine both nutrition and respiration are much simpler in the fœtus; the adult consumes materials and transforms them into work (see *Mechanical equivalent of heat*, p. 78) or heat. The fœtus has to perform no

* 1, Uterus. 2, Intermediate tissue. 3, Placenta (membrana reflexa *seu* caduca serotina), where the maternal and fœtal vessels ramify. (Chailly-Honoré.)

work and expends no force; it has not even to produce heat, it receives that from the mother. It takes alimentary materials only for the building of tissues and the development of organs; consequently the difference in the character of its venous and arterial blood is not very great, and by no means the same as in the arterial and venous blood of adult life. However, oxidation, no matter how feeble it may be, is produced in the embryo; thus, the heart performs its work and must occasion products of combustion; moreover, every formation of tissue is accompanied by phenomena of combustion, which should give rise to excrementitial products. These products are eliminated principally by the liver and urinary organs (first the Wolffian body and then the kidneys); the liver is also very much developed in the embryo, and up to a certain point it may replace the lung as an organ for the excretion of organic waste. A certain amount of urea is also contained in the bladder of the embryo, which is thrown off into the amniotic cavity. Consequently, the amniotic fluid contains at the close of the embryonic life a large number of excrementitial products, because in addition to the urine there are products resulting from the desquamation of the skin.

II. *Development of the body of the embryo.*

If we bear in mind what has preceded in regard to the formation of the umbilical vesicle (pp. 500 and 503) we shall also understand how this vesicle, in consequence of a peculiar strangulation, is separated from the common blastodermic vesicle (p. 587); the borders of the germinal space or area, as well as its cephalic and caudal extremities or hoods, drawn along by this strangulation or constriction, form by their curvatures the sides as well as the cephalic and caudal hoods (Fig. 137, 139, 140), which unite and form a cavity. This cavity might be likened to the hollow or interior of a slipper, and communicates with that of the umbilical vesicle, as we have before stated (Fig. 139, p. 501). This is the *primary cavity of the embryo*, or rather its intestinal cavity (Fig. 137, 12). To complete this rough sketch of embryology we will proceed to the consideration of the two grand systems, the *nervous system* and that of the *circulation.*

a. Central Nervous System. — As soon as the germinal space or area has assumed the form of an elongated spot (like the sole of a slipper) a central longitudinal line, called

the primitive groove, appears; this serves as the point of origin of the central nervous system (spinal cord and encephalon). In fact, this *line* is simply a groove (Fig. 145) bounded by two longitudinal ridges of the external layer or fold (*epiblast*) of the blastoderm. These two ridges (*medullary folds*, Fig. 145, 3) extend backwards and, by their union, surround the *medullary* canal. This canal is represented in the adult by the central canal of the spinal cord with the fourth ventricle and the ventricles of the brain (and the aqueduct of Sylvius). The incomplete closure of this medullary groove results in the formation of the fourth ventricle. It is generally admitted at the present time that the external layer of the blastoderm (*epiblast*) forms only the epithelium of the central canal of the spinal cord (and cerebral ventricles, vibratile epithelium, see p. 190), and that the nerve elements originate in a part of the middle layer (*mesoblast*) subjacent to this epithelium. This view is confirmed by the fact that everywhere else the nerve elements are formed at the expense of the intermediate layer (*mesoblast*).

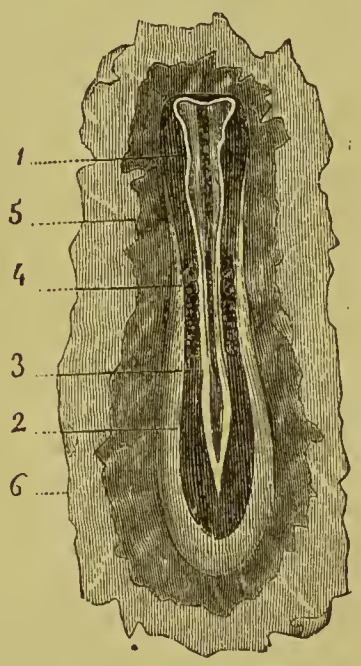


Fig. 145. — Origin of the nervous system.*

The upper portion of the medullary or neural canal forms the encephalic substance; this part swells out into three vesicles (*cerebral vesicles* or *cells*) which are respectively named in order, from front to back: the anterior cerebral, the middle cerebral, and the posterior cerebral cells, or the *first*, *second*, and *third* cerebral vesicles. The *anterior* or *first cerebral cell* or *vesicle* is again divided into two portions, the most anterior of which (anterior of the brain), overlaying the second, forms the cerebral hemispheres and corpus callosum, and the posterior (*intermediate portion of the brain*) forms the thalami optici and the third ventricle (continuation of the medullary canal): 2. The *middle* or *second* cerebral

* 1, Medullary groove. 2, Inferior enlargement of the medullary groove (rhomboid sinus). 3, Crests or medullary folds (laminæ dorsales). 5, Middle and external folds of the blastoderm. 6, Inner fold of the blastoderm (Bischoff).

vesicle is not divided (middle portion of the brain) and forms the region of the corpora quadrigemina with the aqueduct of Sylvius (continuation of the medullary canal); 3. The posterior or third cerebral vesicle divides, like the first, into two portions; one of which, that nearest to the middle part of the brain, will form the protuberance, or medulla oblongata, and the cerebellum (posterior part of the brain); the other of these divisions, a direct continuation of the spinal cord, will form the rachidian bulb (medulla oblongata, strictly speaking); this is the point in which the medullary or neural canal does not completely close, but persists in its original form of a groove and constitutes the floor of the fourth ventricle.

The peripheral nerves are formed in their proper place at the expense of the middle layer (mesoblast) of the blastoderm. The optic nerve and retina form an exception and are represented by a diverticulum of the encephalic substance (see p. 425, Fig. 113.)

The ganglia of the great sympathetic are also formed in their proper places, independently of the cerebro-spinal substance, and from the middle layer (mesoblast) of the blastoderm, as we have already learned, in treating of the semilunar ganglia of the abdominal portion of the sympathetic system (see p. 277).

b. Circulation in the Embryo. — The circulation of the embryo depends upon its method of nutrition. As we have already learned, this nutrition of the embryo may be effected in three different ways: First, by the simple and direct assimilation of the albuminous substance in which the ovum is immersed; no system of circulation is required for this simple form of imbibition. Second, by an assimilation of the contents of the umbilical vesicle; these contents are conveyed to the embryo by a peculiar system which forms the *primary* or *omphalo-mesenteric circulation* (sometimes written *omphalo-mesaraic*). Third, by an interchange with the maternal blood through the placenta; this method of nutrition is fulfilled by the *secondary* or *placental circulation.*

1. The system for the *primary circulation* commences with the formation of the *heart;* this organ is at first represented by a cylinder of embryonic globules; soon the surrounding globules become organized into muscular fibres, whilst those at the centre undergo a partial dissolution and form the first blood. Simultaneously the heart, which at first

was longitudinal, now assumes the form of the letter S (Fig. 146, 4), and commences to contract and propel the blood into the peripheral vessels.

These peripheral vessels, as we have already said, are formed in their proper places and consist, at the first, of *two aortic* arches, which are offshoots from the anterior extremity

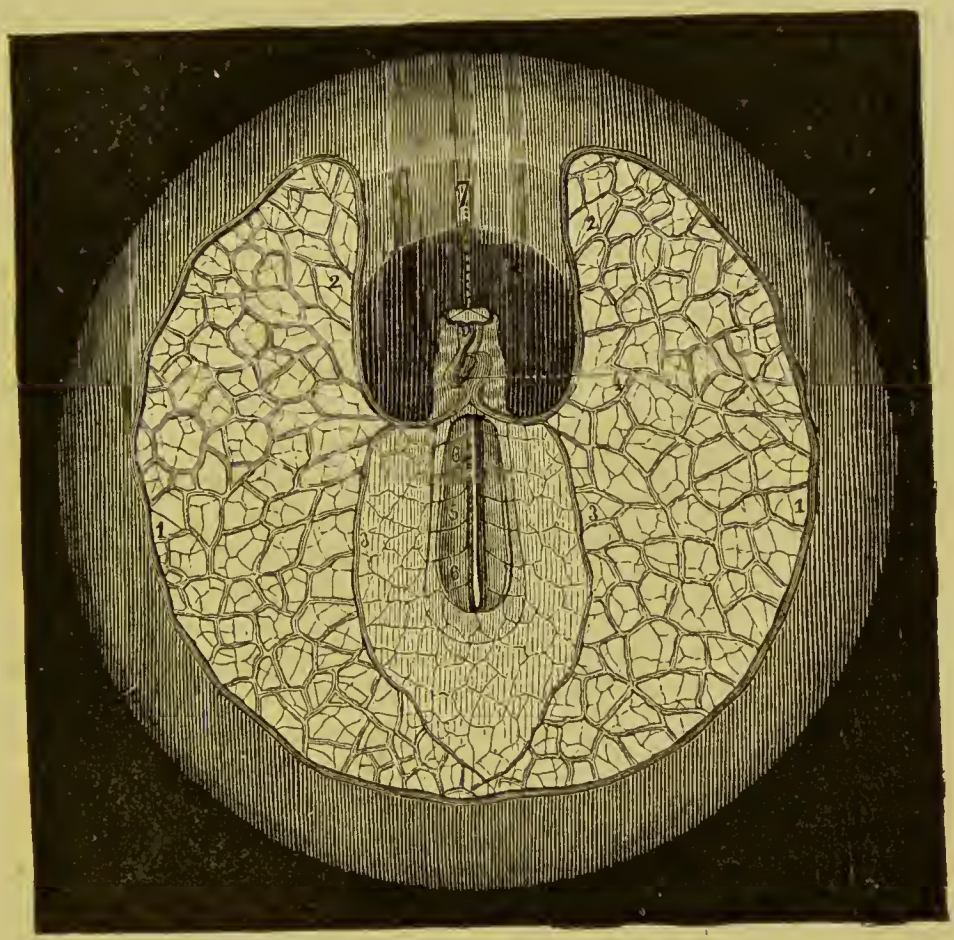


Fig. 146. — Primary circulation.*

of the cardiac tube. These curve around and below the cephalic hood (*anterior vertebral arteries*), unite in a single trunk (*aorta*) at the median portion of the vertebral column, and again divide, descending towards the caudal extremity of the embryo by two branches, the posterior vertebral;

* Germinal area of an embryo; the ventral surface of the embryo is presented. 1, Terminal sinus. 2, Omphalo-mesenteric vein. 3, Its posterior branch. 4, Heart in the form of an S. 5, Primitive aorta, or posterior vertebral arteries. 6, Omphalo-mesenteric arteries. (Bischoff, "Developpement de l'Homme," p. lxiv.)

these will form at a later period, following a posterior direction, the two *iliac arteries*. Numerous arterial branches, the most remarkable of which on account of size are those which go to the intestine and *umbilical vesicle* (Fig. 146, 5), are sent off from the posterior vertebral arteries, and distribute blood to the tissues of the embryo; these two *omphalo-mesenteric arteries* are most essential to the primary circulation (146, 6). The blood goes through them to the walls of the umbilical vesicle, and percolating there in a rich network, which occupies only a portion of this vesicle (*area vasculosa*, Fig. 146), it is charged with the nutritive elements of the yolk, and is afterwards launched into a sinus, which occupies the outside of the *area vasculosa* (*terminal sinus*, sinus venosus, Fig. 146, 1); the blood then returns through two veins (omphalo-mesenteric) to the posterior extremity of the cardiac cylinder (Fig. 146, 2, 3). This primary circulation lasts but a short time in the human embryo, as the functions of the umbilical vesicle soon cease and the vesicle undergoes atrophy (see p. 502); so also at this period the corresponding portion of the omphalo-mesenteric vessels undergo the same fate, the arteries being reduced to *one mesenteric artery*, the veins to *one mesenteric vein*, and thus form the future *vena portæ*.

2. The remainder of the primary circulation, thus modified, and with the addition of new vessels, then forms the secondary or *placental circulation*. We will consider the formation of the organs of this new system, by commencing with the placenta, and the course of the blood towards the heart by the venous system, and its return from the heart of the fœtus to the placenta through the arterial system.

a. Placental Venous System. — The blood that becomes charged in the placenta with constructive elements received from the blood of the mother (see p. 506) goes to the body of the fœtus by two veins which are developed on the pedicle of the allantoïs; these veins pass into the embryo with the umbilicus, whence their name of *umbilical veins*. One of these vessels immediately becomes atrophied, and only one umbilical vein then remains, which unites with the posterior extremity of the heart to form the central end of the mesenteric vein; so that this central end which was primarily the omphalo-mesenteric (*omphalo-mesaraic*) trunk, afterwards the trunk of the mesenteric vein, now represents the common trunk of the umbilical and mesenteric veins (Fig. 149, 1; yet the transformations do not rest here.

A protuberance is formed upon this common trunk which serves for a *vascular blood gland*, or the liver (*glycogenic* portion of the liver, see pp. 232 and 265); so soon as the liver is formed around the common trunk of the umbilical and mesenteric veins, each of these veins sends into this glandular protuberance, or rather pouch, vascular ramifications; those which come from the mesenteric veins form the afferent hepatic veins, and those which come from the common trunk form the efferent hepatic veins. In this way,

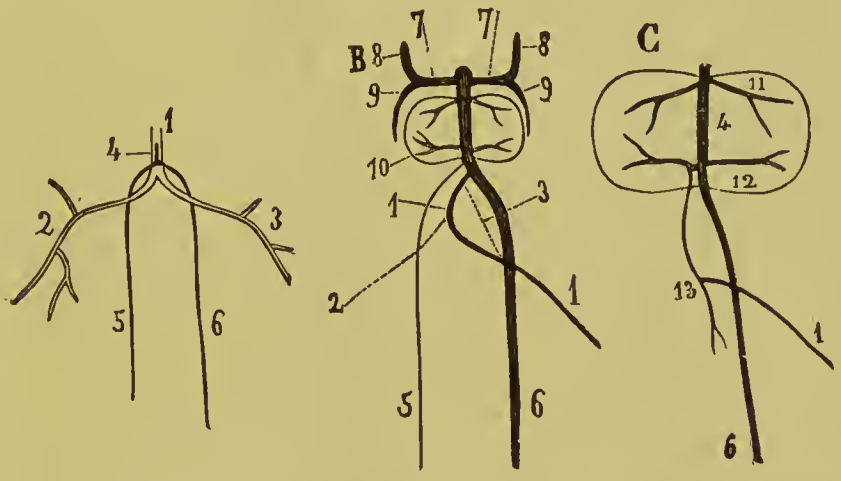


Fig. 147.—Diagram of the development of the omphalo-mesenteric, umbilical, and portal veins.*

and as more clearly indicated in the Fig. 147 (B), the mesenteric vein and its afferent hepatic veins form the portal system, whose veins ramify in the liver and whose subsequent union comprises the efferent hepatic veins; finally, these latter conduct to the common and free trunk beyond the

* A. *Period corresponding with the close of the primary and commencement of the second circulation.*—1, Common trunk of the omphalo-mesenteric veins. 2, Right omphalo-mesenteric vein. 3, The left. 4, Common trunk of the umbilical veins in process of formation. 5, The right umbilical vein. 6, The left.

B. *Formation of the liver.*—1, Permanent mesenteric vein (future portal vein). 2, 3, Representing the place of the atrophied omphalo-mesenteric veins. 5, Right umbilical vein undergoing a process of atrophy. 6, Permanent umbilical vein. 7, Canal of Cuvier (ductus Cuvieri). 8, Anterior or superior cardinal veins. 9, Posterior or inferior cardinal veins, or jugular veins. 10, Liver, with the afferent and efferent veins.

C. *Formation of the vena porta and canalis Arantii seu ductus venosus* (perfected state of the placental circulation). 1, Remains of the omphalo-mesenteric (omphalo-mesaraic) vein. 13, Mesenteric vein (portal vein). 6, Umbilical vein. 4, Ductus venosus *seu* canalis Arantii. 12, Afferent hepatic veins. 11, Efferent hepatic veins. (Kölliker.)

liver. This portion of the old trunk afterwards forms the upper part of the inferior vena cava, whose lower portion is

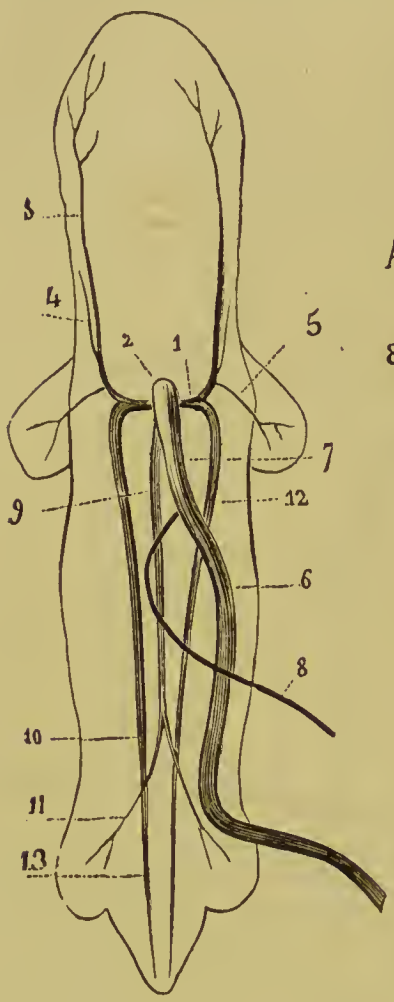


Fig. 148. — Venous system of the embryo.*

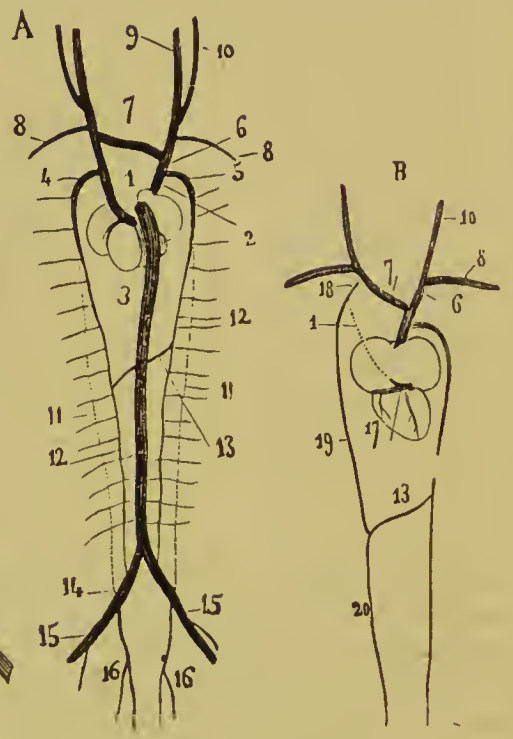


Fig. 149. — Formation of the true or permanent venous system.†

* 1, Duct of Cuvier. 2, Place where all the veins unite and pour their contents into the inferior extremity of the heart (future auricle). 3, Anterior cardinal vein. 6, Umbilical vein. 7, The same vein near the liver (which is not in the plate, neither the afferent and efferent hepatic veins). 8, Omphalo-mesenteric vein. 9, Inferior vena cava. 12, Posterior cardinal veins. Kölliker, "Entwickelungsgeschichte.")

† A. *Period of formation.* — 1, Left superior vena cava. 2, Right superior vena cava. 3, Inferior vena cava. 4, 5, Inferior cardinal veins (future azygos). 7, Anastomosis between the two anterior cardinal veins, future left brachio-cephalic trunk. 8, 9, 10, Future jugular and subclavian veins.

B. *Permanent venous trunks* (as in the adult). — These vessels (as in the Fig. A) are represented as if looking at the posterior portion of the body. 1, Obliterated left superior vena cava. 6, Right vena innominata. 7, Left vena innominata. 8, Subclavian. 13, Trunk of the hemi-azygos. 18, Left superior intercostal. 19, 20, Superior and inferior portions of the left azygos.

completed by a development of a trunk which collects the blood that comes from the undeveloped lower limbs. The ductus venosus (canalis Arantii) and the sinus venosus are formed of that portion of the umbilical and mesenteric veins, which lies between the confluence of the afferent hepatic and efferent hepatic veins (Fig. 147, B and C, 4).

We will not insist upon the ulterior results of this arrangement, which is one of the most complicated points in the anatomy of the liver. It is only necessary to understand that the umbilical vein, when it arrives at the liver, pours a part of its contents into the portal vein (into the left portion of the portal vein), and conveys another portion through the ductus venosus directly into the lower vena cava, and thence to the heart.

The veins which collect the blood from the body of the embryo (anterior, or superior, and posterior, or inferior, cardinal, and lower vena cava, see Fig. 148) empty their contents simultaneously and on each side, into a common duct (canalis Cuvieri). But this arrangement does not long continue; for soon the posterior, or inferior, cardinal veins become partially atrophied, and the only trace of their existence is found in the azygos veins (large and small azygos, see Fig. 149, B). Between the anterior cardinal veins a transverse duct (left brachio-cephalic, 7, A and B, Fig. 149) is formed, simultaneously with the atrophy of the left Cuverian duct. On the other hand, the right duct of Cuvier persists and becomes the superior vena cava (Fig. 149, A, 6). We thus understand the arrangement of the right azygos vein (large azygos) which in the adult conducts the blood into the superior vena cava, since it represents the central end of the right posterior cardinal vein; as well as the arrangement of the right brachio-cephalic trunk, which represents the central end of the right superior cardinal vein. At this period of embryonic existence the inferior and superior venæ cavæ empty their contents into the heart by a common trunk, while at a later period of its existence this common trunk gradually becomes a portion of the wall of the auricular cavity; so that, after a while, the two venæ cavæ separately connect with the auricle (as in the adult) at a little distance from each other.

b. Heart. — The central organ of circulation, at first represented in the form of a simple and cylindrical tube, afterwards resembling the letter S (Fig. 146), becomes divided by means of increasing constrictions into three cavities, viz., the auricular, ventricular, and arterial (aortic bulb or sinus,

bulbus arteriosus). The curvature of the heart gradually increases in such a manner that the ventricle, which at first was placed above, turns downwards and forwards, and the auricle upwards and backwards. Simultaneously with the establishment of the placental circulation, a median partition, or septum, originates at the apex of the ventricle, whose extension finally divides the single ventricular cavity into two cavities, called the right and left ventricle. A partition is also formed in the large sinus of the aorta (bulbus arteriosus), the latter having assumed a spiral form; this partition divides the sinus into two ducts which are twisted on their axes; one of these ducts communicates with the right ventricle (the origin of the pulmonary artery) and the other with the left ventricle, which latter becomes the origin of the aorta.

The auricular cavity is also gradually divided into a right and a left auricle, by a septum which originates at the auriculo--ventricular region. Yet during the remainder of the fœtal existence, this incomplete partition or septum contains an opening (*foramen Botalis* seu *ovale*) which allows of a communication between the two auricles. The relations of this inter-auricular opening, with the mouths of the venæ cavæ in the right auricle, form a characteristic feature of the placentary circulation. The mouth, or opening, of the inferior vena cava is provided with the Eustachian valve; this valve is largely developed at this period, and is so arranged that the blood which comes from the inferior vena cava can only go through the postero-inferior portion of the right auricle, and is directed towards the inter-auricular opening; by this means the blood is diverted through the foramen ovale into the left auricle, and thence into the left ventricle, etc. (see farther on). On the other hand, the blood which comes from the superior vena cava, there being no such valve here, passes from the right auricle (which it fills, just as in adult age) by the auriculo-ventricular orifice directly into the right ventricle, etc. (see also farther on).

c. Arteries. — We have spoken of two branches that originate from the anterior extremity of the cardiac tube; these soon turn towards the back and form what is called the first pair of aortic arches (see p. 511). Soon afterwards two or three other aortic arches are successively developed, and are behind this first aortic arch; these also unite in the median trunk of the descending portion of the aorta (Fig. 150); yet the continuance of these arches is only very transitory, and most of them are soon obliterated, some of their branches

alone remaining to form the large and permanent branches of the circulation. In this way the highest of these arches becomes the right brachio-cephalic (arteria innominata), the carotid, and the left subclavian arteries (Fig. 150, 5, 4); on the right side the second arch disappears, but, on the left, it forms the arch of the permanent aorta (3); the third sends off on each side a branch which ramifies through the lung of the corresponding side; while, on the right, the portion beyond this offshoot becomes atrophied, and its companion on the left side remains and furnishes a communication between the pulmonary artery and the arch of the aorta; this is called the *ductus arteriosus*. This ductus arteriosus holds the same relation to the placental circulation as the foramen ovale (of Botal) and the ductus venosus (of Arantius) (see p. 515).

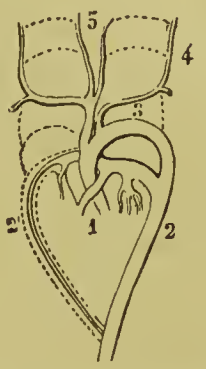


Fig. 130.—Aortic arches and permanent arterial trunks.*

The bulb of the aorta, moreover, is so divided that the part of its cavity, which communicates with the left ventricle, is a continuation of the remains of the two first pairs of aortic arches (carotids, subclavians, and arch of the permanent aorta); whilst that part of its cavity, which communicates with the right ventricle, is a continuation of the remains of the third aortic arch, the pulmonary artery (and the ductus arteriosus) (Fig. 150, 1).

If we pursue the arrangement of the arterial system from centre to the periphery, we shall find that the descending portion of the aorta gradually elongates (p. 512), and that the two posterior vertebral arteries become the *iliac arteries;* from these latter are given off two, relatively, very large branches, which are called the *umbilical arteries;* these following the pedicle of the allantoïs, and entwining around the single umbilical vein in the umbilical cord, convey blood from the fœtus towards the placenta; at this point the blood is distributed in the capillaries of the villi, and comes into

* 1, Trunks which spring from each ventricle (bulbus arteriosus dividing into the origin of the aorta and origin of the pulmonary artery); above, five pairs of aortic arches may be seen; the highest of these disappear; only the three which are nearest the heart become permanent vessels, and represent the subclavian, the right, and the left carotid arteries 5, 4. 3, The arch of the aorta. 2, The descending portion of the aorta; the ductus arteriosus, which has only a very transitory existence, may be seen at the junction of the arch of the aorta with its descending portion.

those relations of interchange with the blood of the mother already spoken of (p. 507). We have now returned to the point from which we set out, and have successively passed through the various segments of the circle of the placental circulation. We are now prepared to review in a brief space, and present a summary of the method by which the blood moves through the vessels, from the fœtus to the placenta, and from the placenta to the fœtus; also how this placental circulation mingles with the circulation in the different parts of the embryo (head, limbs, and viscera).

Summary. — The blood comes from the placenta through the umbilical vein and goes to the lower surface of the liver, thence it is returned into the lower vena cava by two different channels; a portion returns directly to the lower vena cava through the ductus venosus of Arantius; the other portion goes through the left branch of the portal vein, is distributed in the left lobe of the liver, whence it flows through the corresponding hepatic veins to the lower vena cava; it may be noticed that the left lobe of the liver, by this arrangement, receives a mixture of intestinal venous blood (portal vein) and a blood, which has been vivified by its passage through the placenta (umbilical vein), whilst the right lobe receives only the intestinal blood. This explains the increased size and development of the left lobe; since the preponderance of the lobes is reversed in the liver of adult age.

The blood from the inferior vena cava passes into the right auricle; yet it apparently only skims through this cavity without being mingled with the blood from the superior vena cava. In fact (see p. 516), the blood of the inferior vena cava, guided by the Eustachian valve, passes through the foramen ovale into the left auricle, thence into the left ventricle, and so into the arch of the aorta. At the last-named place a small part of this blood is taken by the descending portion of the aorta, where we shall presently find it mingling with the blood furnished by the ductus arteriosus; the larger part of the blood received into the arch of the aorta traverses the brachio-cephalic (innominate), the carotid, and subclavian trunks, for the purpose of furnishing nutrition for the head and arms. Let us not forget that this blood, thus supplied to the upper extremities of the embryo, is almost wholly arterial, that is to say, has been vivified by the placental hæmatosis, with scarcely any venous blood (only that from the inferior vena cava and the hepatic

veins). Having become venous, this blood from the head and upper extremities returns through the superior vena cava to the right auricle, thence to the right ventricle (see p. 516) and the pulmonary artery. Since the lung at this period forms a compact mass, and scarcely permeable, the blood of the pulmonary artery passes directly into the ductus arteriosus, and thence down the descending portion of the aorta, where it mingles with that small amount of arterial blood, which is not sent from the arch of the aorta to the lower extremities of the fœtus. Having arrived at the primary iliac arteries, a large amount of the blood is diverted through the umbilical arteries for the purpose of undergoing hæmatosis in the placenta, whilst a smaller amount continues on its course through the iliacs, in order to nourish the pelvis and lower extremities of the fœtus.

Respecting the character of the blood, which the different portions of the body of the embryo receive, it may be noticed that its upper part receives arterial, mixed with a small quantity of venous blood; whilst the parts below the umbilicus receive venous, mixed with a small quantity of arterial blood. This difference corresponds with what we have mentioned in respect to the two lobes of the liver, and explains the preponderance of size, and increased development, of the upper over the lower part of the body of the embryo.

This *placental* or *secondary circulation*, with its mode of nutrition and respiration to which it is adapted, continues until the birth of the embryo. At this latter stage the placental circulation ceases, and is replaced by the functions of nutrition and respiration which we have already studied in the adult. The disappearance of the secondary circulation follows the same order that we have just studied: first, the placenta, which is thrown off after the expulsion of the fœtus (under the name of after-birth); then the umbilical vein, which is cut and obliterated by the teeth of animals, or by direct section after ligation in mankind. That portion of this vein, which goes from the umbilicus to the liver, is also obliterated by a retraction of its sides, as also the ductus venosus of Arantius; these vessels are replaced by the fibrous ligaments which we have studied in descriptive anatomy. The Eustachian valve in the heart undergoes atrophy, the foramen ovale is obliterated, and the two auricles thenceforth are separated; the right auricle transmits to the right ventricle the blood from the inferior vena cava as well as that from the superior vena cava.

Moreover, the lung becomes permeable and the ductus arteriosus atrophied; the blood from the right ventricle goes directly to the lungs. Finally, the umbilical arteries are obliterated by hypertrophy and retraction of their sides, and are represented by the fibrous ligaments found on the walls of the bladder; the aorta carries the blood only to the limbs, to the surface of the body, and to the viscera; the two circles of the permanent circulation, with complete independence of each other, are then formed.

APPENDIX.

COMPARISON OF THE THERMOMETRIC SCALES.

The following rules will be found convenient for translating the degrees of one scale into those of another:—

1. To reduce Centigrade degrees to those of Fahrenheit, multiply by 9, and divide by 5, and to the quotient add 32; that is,—

$$\frac{\text{Cent.} \times 9}{5} + 32 = \text{Fahr.}$$

2. To reduce Fahrenheit's degrees to Centigrade:—

$$\frac{\text{Fahr.} - 32 \times 5}{9} = \text{Cent.}$$

Fahrenheit.	Centigrade.	Fahrenheit.	Centigrade.	Fahrenheit.	Centigrade.	Fahrenheit.	Centigrade.
212	100	195	90.5	177.8	81	160	71.1
211	99.4	194	90	177	80.5	159.8	71
210.2	99	193	89.4	176	80	159	70.5
210	98.9	192.2	89	175	79.4	158	70
209.7	98.7	192	88.8	174.2	79	157	69.4
209	98.3	191.7	88.7	174	78.8	156.2	69
208.4	98	191	88.3	173.7	78.7	156	68.9
208	97.8	190.4	88	173	78.3	155.7	68.7
207.5	97.5	190	87.8	172.4	78	155	68.3
207	97.2	189.5	87.5	172	77.7	154.4	68
206.6	97	189	87.2	171.5	77.5	154	67.7
206	96.6	188.6	87	171	77.2	153.5	67.5
205.2	96.2	188	86.6	170.6	77	153	67.2
205	96.1	187.2	86.2	170	76.6	152.6	67
204.8	96	187	86.1	169.2	76.2	152	66.6
204	95.5	186.8	86	169	76.1	151.2	66.2
203	95	186	85.5	168.8	76	151	66.1
202	94.4	185	85	168	75.5	150.8	66
201.2	94	184	84.4	167	75	150	65.5
201	93.9	183.2	84	166	74.4	149	65
200.7	93.7	183	83.9	165.2	74	148	64.4
200	93.3	182.7	83.7	165	73.9	147.2	64
199.4	93	182	83.3	164.7	73.7	147	63.9
199	92.7	181.4	83	164	73.3	146.7	63.7
198.5	92.5	181	82.7	163.4	73	146	63.3
198	92.2	180.5	82.5	163	72.7	145.4	63
197.6	92	180	82.2	162.5	72.5	145	62.7
197	91.6	179.6	82	162	72.2	144.5	62.5
196.2	91.2	179	81.6	161.6	72	144	62.2
196	91.1	178.2	81.2	161	71.6	143.6	62
195.8	91	178	81.1	160.2	71.2	143	61.6

Fahrenheit.	Centigrade.	Fahrenheit.	Centigrade.	Fahrenheit.	Centigrade.	Fahrenheit.	Centigrade.
142.2	61.2	115	46.1	87.8	31	60	15.5
142	61.1	114.8	46	87	30.5	59	15
141.8	61	114	45.5	86	30	58	14.4
141	60.5	113	45	85	29.4	57.2	14
140	60	112	44.4	84.2	29	57	13.8
139	59.4	111.2	44	84	28.9	56.7	13.7
138.2	59	111	43.9	83.7	28.7	56	13.3
138	58.8	110.7	43.7	83	28.3	55.4	13
137.7	58.7	110	43.3	82.4	28	55	12.7
137	58.3	109.4	43	82	27.7	54.5	12.5
136.4	58	109	42.7	81.5	27.5	54	12.2
136	57.7	108.5	42.5	81	27.2	53.6	12
135.5	57.5	108	42.2	80.6	27	53	11.6
135	57.2	107.6	42	80	26.6	52.2	11.2
134.6	57	107	41.6	79.2	26.2	52	11.1
134	56.6	106.2	41.2	79	26.1	51.8	11
133.2	56.2	106	41.1	78.8	26	51	10.5
133	56.1	105.8	41	78	25.5	50	10
132.8	56	105	40.5	77	25	49	9.4
132	55.5	104	40	76	24.4	48.2	9
131	55	103	39.4	75.2	24	48	8.9
130	54.4	102.2	39	75	23.8	47.7	8.7
129.2	54	102	38.9	74.7	23.7	47	8.3
129	53.9	101.7	38.7	74	23.3	46.4	8
128.7	53.7	101	38.3	73.4	23	46	7.7
128	53.3	100.4	38	73	22.7	45.5	7.5
127.4	53	100	37.7	72.5	22.5	45	7.2
127	52.7	99.5	37.5	72	22.2	44.6	7
126.5	52.5	99	37.2	71.6	22	44	6.6
126	52.2	98.6	37	71	21.6	43.2	6.2
125.6	52	98	36.6	70.2	21.2	43	6.1
125	51.6	97.2	36.2	70	21.1	42.8	6
124.2	51.2	97	36.1	69.8	21	42	5.5
124	51.1	96.8	36	69	20.5	41	5
123.8	51	96	35.5	68	20	40	4.4
123	50.5	95	35	67	19.4	39.2	4
122	50	94	34.4	66.2	19	39	3.9
121	49.4	93.2	34	66	18.8	38.7	3.7
120.2	49	93	33.9	65.7	18.7	38	3.3
120	48.9	92.7	33.7	65	18.3	37.4	3
119.7	48.7	92	33.3	64.4	18	37	2.7
119	48.3	91.4	33	64	17.7	36.5	2.5
118.4	48	91	32.7	63.5	17.5	36	2.2
118	47.7	90.5	32.5	63	17.2	35.6	2
117.5	47.5	90	32.2	62.6	17	35	1.6
117	47.2	89.6	32	62	16.6	34.2	1.2
116.6	47	89	31.6	61.2	16.2	34	1.1
116	46.6	88.2	31.2	61	16.1	33.8	1
115.2	46.2	88	31.1	60.8	16	33	0.5
						32	0

The weight of the Kilogramme is settled by Act of Parliament to be equal to 15432.3487 *English grains; but according to the U. S. Pharmacopeia it is equal to* 15,434.023 *or about* ℔ ij ℥ viij.

COMPARISON OF THE METRICAL WITH THE COMMON MEASURES.

By Dr. Warren De La Rue.

MEASURES OF LENGTH.

	In English Feet = 12 Inches.	In English Yards = 3 Feet.	In English Miles = 1,760 Yards.
Millimetre	0.0032809	0.0010936	0.0000006
Centimetre	0.0328090	0.0109363	0.0000062
Decimetre	0.3280899	0.1093633	0.0000621
Metre	3.2808992	1.0936331	0.0006214
Decametre	32.8089920	10.9363310	0.0062138
Hectometre	328.0899200	109.3633100	0.0621382
Kilometre	3280.8992000	1093.6331000	0.6213824
Myriometre	32808.9920000	10936.3310000	6.2138244

1 Inch = 2.539954 Centimetres. 1 Yard = 0.91438348 Metre.
1 Foot = 3.0479449 Decimetres. 1 Mile = 1.6093149 Kilometres.

MEASURES OF SURFACE.

1 Square Inch = 6.4513669 Square Centimetres.
1 Square Foot = 9.2899683 Square Decimetres.
1 Square Yard = 0.83609715 Square Metre or Centaire.
1 Acre = 0.404671021 Hectare.

MEASURES OF CAPACITY.

	In Cubic Inches.	In Cubic Ft. = 1,728 Cubic In.	In Pints = 34.65923 Cubic In.	In Gallons = 8 Pints = 277.27384 Cubic In.	In Bushels = 8 Gallons = 2218.19075 Cubic In.
Millilitre, or cubic centimetre	0.061027	0.0000353	0.001761	0.00022010	0.000027512
Centilitre, or 10 cubic centimetres	0.610271	0.0003532	0.017608	0.00220097	0.000275121
Decilitre, or 100 cubic centimetres	6.102705	0.0035317	0.176077	0.02200967	0.002751208
Litre, or cubic decimetre	61.027052	0.0353166	1.760773	0.22009668	0.027512085
Decalitre, or centistere	610.270515	0.3531658	17.607734	2.20096677	0.275120846
Hectolitre, or decistere	6102.705152	3.5316581	176 077341	22.00966767	2.751208459
Kilolitre, or stere, or cubic metre	61027.051519	35.3165807	1760 773414	220.09667675	27.512084594
Myriolitre, or decastere	610270.515194	353.1658074	17607.734140	2200.96676750	275.120845937

1 Cubic Inch = 16.3861759 Cubic Centimetres.
1 Cubic Foot = 28.3153119 Cubic Decimetres.
1 Gallon = 4.543457969 Litres.

MEASURES OF WEIGHT.

	In English Grains.	In Troy Ounces = 480 Grains.	In Avoirdupois Lbs. = 7,000 Grains
Milligramme	0.015432	0.000032	0.0000022
Centigramme	0 154323	0 000322	0.0000220
Decigramme	1.543235	0.003215	0.0002205
Gramme	15.432349	0.032151	0.0022046
Decagramme	154.323488	0.321507	0.0220462
Hectogramme	1543.234880	3.215073	0.2204621
Kilogramme	15432.348800	32.150727	2.2046213
Myriogramme	154323.488000	321.507267	22.0462126

1 Grain = 0.06479895 Gramme.
1 Troy Oz.= 31.103496 Grammes.
1 Lb. Avd.= 0.45359265 Kilogramme.

NOTE. — These tables are taken from "Lessons in Elementary Chemistry," by H. E. Roscoe, B.A., F.R.S.

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